

QL

1

R454

NH

S

de la
SOCIÉTÉ SUISSE DE ZOOLOGIE
et du
MUSÉUM D'HISTOIRE NATURELLE
de la Ville de Genève

tome 120
fascicule 2
2013



GENÈVE JUIN 2013 ISSN 0035 - 418 X

SWISS JOURNAL OF ZOOLOGY

REVUE SUISSE DE ZOOLOGIE

REVUE SUISSE DE ZOOLOGIE

TOME 120— FASCICULE 2

Publication subventionnée par:
ACADÉMIE SUISSE DES SCIENCES NATURELLES (SCNAT)
VILLE DE GENÈVE
SOCIÉTÉ SUISSE DE ZOOLOGIE

Comité de rédaction

JACQUES AYER

Directeur du Muséum d'histoire naturelle de Genève

ALICE CIBOIS, PETER SCHUCHERT

Chargés de recherche au Muséum d'histoire naturelle de Genève

Comité de lecture

A. Cibois (oiseaux), G. Cuccodoro (coléoptères), S. Fisch-Muller (poissons),
B. Merz (insectes, excl. coléoptères), J. Mariaux (invertébrés excl. arthropodes),
M. Ruedi (mammifères), A. Schmitz (amphibiens, reptiles), P. Schwendinger
(arthropodes excl. insectes).

Le comité soumet chaque manuscrit pour évaluation à des experts d'institutions suisses ou étrangères selon le sujet étudié.

La préférence sera donnée aux travaux concernant les domaines suivants: taxonomie, systématique, faunistique, phylogénie, évolution, morphologie et anatomie comparée.

Administration

MUSÉUM D'HISTOIRE NATURELLE
1211 GENÈVE 6

Internet: <http://www.ville-ge.ch/musinfo/mhng/page/rsz.htm>

PRIX DE L'ABONNEMENT:

SUISSE Fr. 225.—

UNION POSTALE Fr. 250.—
(en francs suisses)

Les demandes d'abonnement doivent être adressées
à la rédaction de la *Revue suisse de Zoologie*,
Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Suisse

ANNALES

de la
SOCIÉTÉ SUISSE DE ZOOLOGIE
et du
MUSÉUM D'HISTOIRE NATURELLE
de la Ville de Genève

tome 120
fascicule 2
2013



REVUE SUISSE DE ZOOLOGIE

TOME 120— FASCICULE 2

Publication subventionnée par:
ACADÉMIE SUISSE DES SCIENCES NATURELLES (SCNAT)
VILLE DE GENÈVE
SOCIÉTÉ SUISSE DE ZOOLOGIE

Comité de rédaction

JACQUES AYER
Directeur du Muséum d'histoire naturelle de Genève

ALICE CIBOIS, PETER SCHUCHERT
Chargés de recherche au Muséum d'histoire naturelle de Genève

Comité de lecture

A. Cibois (oiseaux), G. Cuccodoro (coléoptères), S. Fisch-Muller (poissons),
B. Merz (insectes, excl. coléoptères), J. Mariaux (invertébrés excl. arthropodes),
M. Ruedi (mammifères), A. Schmitz (amphibiens, reptiles), P. Schwendinger
(arthropodes excl. insectes).

Le comité soumet chaque manuscrit pour évaluation à des experts d'institutions suisses ou étrangères selon le sujet étudié.

La préférence sera donnée aux travaux concernant les domaines suivants: taxonomie, systématique, faunistique, phylogénie, évolution, morphologie et anatomie comparée.

Administration

MUSÉUM D'HISTOIRE NATURELLE
1211 GENÈVE 6

Internet: <http://www.ville-ge.ch/musinfo/mhng/page/rsz.htm>

PRIX DE L'ABONNEMENT:

SUISSE Fr. 225.—

UNION POSTALE Fr. 250.—
(en francs suisses)

Les demandes d'abonnement doivent être adressées
à la rédaction de la *Revue suisse de Zoologie*,
Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Suisse

Acanthocephala including the descriptions of new species of *Centrorhynchus* (Centrorhynchidae) and the redescription of *Lueheia inscripta* (Westrumb, 1821) (Plagiorhynchidae) from birds from Paraguay South America

Lesley R. SMALES

Parasitology Section, South Australian Museum, North Terrace Adelaide 5000, South Australia, Australia. Email: l.warner@cqu.edu.au

Acanthocephala including descriptions of new species of *Centrorhynchus* (Centrorhynchidae) and the redescription of *Lueheia inscripta* (Westrumb, 1821) (Plagiorhynchidae) from birds from Paraguay South America. - Acanthocephalans from bird hosts that could not be identified are listed. Centrorhynchidae, including *Centrorhynchus guira* Lunaschi & Drago, 2010 and four new species *C. geranoaeti*, *C. millerae*, *C. pitangi* and *C. viarius* are reported from Paraguay for the first time. Two additional new species, centrorhynchids, were identified but could not be described fully because of insufficient material. The new species are distinguished from congeners principally by the characters of the proboscis armature and further by a combination of the morphometrics of the organs in the trunk, including the male reproductive system, and the size of the eggs. *Lueheia inscripta* (Westrumb, 1821) is reported from Paraguay for the first time and redescribed. The taxonomic position of *C. opimus* is confirmed, *Centrorhynchus polymorphus* is considered a junior synonym of *Sphaerirostris polymorphus* and *Lueheia karachiensis* declared *incertae sedis*.

Keywords: Parasite - Acanthocephala - *Centrorhynchus* - *Lueheia* - South America - Paraguay - birds.

INTRODUCTION

The Acanthocephala from South American birds have not been extensively studied and there has been only a single report, *Centrorhynchus albidus* Meyer, 1933 from a falcon, from Paraguay (Golvan, 1956). An analysis of the family Centrorhynchidae has shown that 10 other species of *Centrorhynchus*, namely *C. crotophagicola* Schmidt & Neiland, 1966, *C. giganteus* Travassos, 1921, *C. guira* Lunaschi & Drago, 2010, *C. kuntzi* Schmidt & Neiland, 1966, *C. microcephalus* (Bravo-Hollis, 1947), *C. nicaraguensis* Schmidt & Neiland, 1966, *C. opimus* (Travassos, 1921), *C. polymorphus* Travassos, 1926, *C. simplex* Meyer, 1932 and *C. tumidulus* (Rudolphi, 1819) are known from Central and South America; Argentina, Brazil, Mexico, Nicaragua, Panama, Paraguay, Puerto Rico, Uruguay and Venezuela (Petroschenko, 1958; Whittaker *et al.*, 1970a; Vicente *et al.*, 1983; Vizcaino, 1993; Golvan, 1994;

Lunaschi & Drago, 2010). Reassigned from *Centrorhynchus* to *Sphaerirostris* by Golvan (1956, 1960) and then returned to *Centrorhynchus* by Golvan (1994), the status of *C. opimus* is discussed below. The position of *C. polymorphus* also needs consideration. Both Dimitrova & Gibson (2005) and Lunaschi & Drago (2010) have suggested that it might better fit the genus *Sphaerirostris* than the genus *Centrorhynchus*.

Two genera of the Plagiorhynchidae, *Plagiorhynchus* and *Lueheia* are found in South American birds but there have been no previous reports of plagiorhynchids from Paraguay. Four species of *Plagiorhynchus* have been described from Brazil (Travassos, 1926) but not reported on since. Two species of *Lueheia*, *L. lueheia* Travassos, 1921 and *L. inscripta* (Westrumb, 1821), were originally described from Brazil (Travassos, 1921, 1926). *Lueheia inscripta* was subsequently reported from Mexico, Nicaragua, Panama and Puerto Rico (Schmidt & Neiland, 1966; Acholonu, 1976; Whittaker *et al.*, 1970b; Golvan, 1994; Calegaro-Marques & Amato, 2010; Salgado-Maldonado & Caspeta-Mandujano, 2010) and a third species, *L. cajabambensis* Machado-Filho & Nicanor-Ibáñez, 1967 was reported from Peru (Machado-Filho & Nicanor-Ibáñez, 1967; Tantaleán *et al.*, 2005). A fourth species, *L. adluheia* (Werby, 1938) has been described from the United States of America (Werby, 1938) and accepted as valid by Van Cleave & Williams (1951), Amin (1985), Golvan (1994), Aly Khan *et al.* (2005) and Salgado-Maldonado & Caspeta-Mandujano (2010) but placed as a synonym of *L. inscripta* by Van Cleave (1942), Yamaguti (1963), Schmidt & Neiland (1966) and Schmidt & Kuntz (1967). Each of the above species occurs in passerine bird hosts. Recently a fifth species, *L. karachiensis* Aly Khan, Bilqees & Muti-ur-Rehman, 2005, has been described from a raptor, *Accipiter badius cenchroides* (Seretzov, 1873) from India. The validity or otherwise of these latter two species needs further consideration given the lack of agreement by various authors with regard to *L. adluheia* and that *L. karachiensis* is geographically isolated from other species of *Lueheia* and not found in a passerine host.

Between 1982 and 1989 the Muséum d'Histoire Naturelle, Geneva (MHNG) sponsored a series of surveys of the vertebrate fauna of Paraguay. As part of this programme acanthocephalans were collected from eight orders of birds comprising 46 species from 11 families. In this paper acanthocephalans from the families Centrorhynchidae and Plagiorhynchidae are documented, new host and geographic records are reported, new species of *Centrorhynchus* are described and the systematic position of *C. opimus* and *C. polymorphus* and the validity of *L. adluheia* and *L. karachiensis* are discussed.

MATERIALS AND METHODS

The birds examined included 36 individuals of 26 species from 17 families from which plagiorhynchids, centrorhynchids and specimens that could not be fully identified were dissected. The collection localities of the hosts, with the number of hosts in parentheses, were as follows:

Alto Paraguay Department General Diaz (1). – Alto Parana Department Itaipu (1). – Boqueron Department Pratt's Gill (1); Pedro P Pena (1); Route Montani –Madrigon 2 (1). – Concepcion Department Aquidaban (1); Santa Sofia 10E (1);

Arroyo Tagatiya-Guazu (1); Puente Zinho (1); Arroyo Tagatija-Mi (1). – Cordillera Department Rio Piribebuy (1); Tobati (1). – Itapua Department Arroyo Agua-Pey (4); Santa Maria (1). – Central Department S-Lorenzo N 10e (6). – Paraguari Department 15 Km E From Cerrito (1). – Presidente Hayes Department Transchaco 70 (1); Transchaco 110 (1); Transchaco 115 (1); Transchaco 180 (1); Transchaco 293 (3); Puerto Militar 35 (1); Pozo Arias (1). – San Pedro Department Arroyo Tapiracuai (1); Rio Guazu, Rte 3, Jejui (2).

On dissection all specimens were fixed with neutral buffered 4% formalin and stored in 75% ethanol. Before microscopic examination all specimens were cleared in lactophenol or beechwood creosote to be studied as wet mounts. All measurements made using an eyepiece micrometer are given in micrometres, unless otherwise stated, with the range followed by the mean in parentheses. Measurements of the neck were taken from the base of the proboscis to the level just anterior to the insertion of the lemnisci and measurements of proboscis width at the widest part anterior to the insertion of the proboscis receptacle. Illustrations were made with the aid of a drawing tube.

The terminology for describing proboscis hook types follows Lunaschi & Drago (2010): that is – true hooks with roots with or without manubria, transitional hooks with manubria and without roots and spiniform hooks without manubria or roots. Where the presence or absence of transitional hooks is not noted in the description all hooks other than true hooks are counted as spiniform hooks, following Schmidt & Neiland (1966). All specimens collected for this study are registered in the MHNG.

RESULTS

Of the acanthocephalans centrorthynchids, all *Centrorthynchus* spp., were found in 16 hosts and a plagiorhynchid, *Lueheia inscripta*, in 5 hosts (Table 1). A further 9 hosts were infected with adult acanthocephalans, specimens that had damaged, missing or inverted proboscides and could not therefore be identified further. Six hosts were infected with cystacanths, some of which could be identified as *Centrorthynchus* spp. (Table 2). All these records are new host and locality records.

Family Centrorthynchidae

A single juvenile male, *Centrorthynchus* sp. 1, was found in *Herpetotheres cachimans* (Linnaeus, 1758); Paraguay, Santa Sofia 10E, 11.10.1988 (INVE 38398). The measurements were as follows: Trunk 3 mm long, 435 at widest part, proboscis 600 long, 215 wide, neck 165 by 215, proboscis receptacle 871 by 188, the lemnisci tubular, extending posteriorly beyond the proboscis receptacle, 1220 long and the testes; anterior 82.5 by 56, posterior 89 by 19.5. The proboscis was armed with 26 rows of 24 hooks per row comprising 6 true hooks + 16 spiniform hooks.

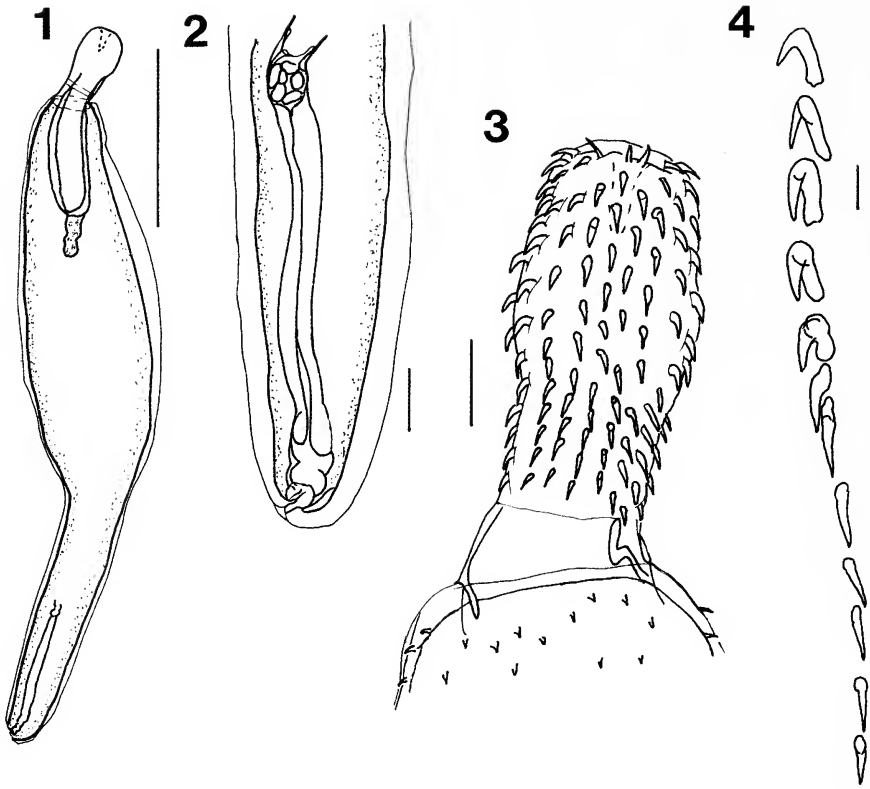
A single juvenile female, also a centrorthynchid, (Figs 1-4) was found in *Turdus amaurochalinus* Cabanis, 1850; Paraguay, S-Lorenzo N 10E 16.10.1987 (MHNG-INV-82726). Since the anterior trunk of this specimen had 2 irregular rows of small spines although otherwise conforming to the diagnosis of the genus *Centrorthynchus* it could not be assigned to any known genus at this time. Measurements were: Trunk length 4.3 mm, maximum width 850; proboscis 617 long by 201 wide; neck 207 by

TABLE 1. Acanthocephala: Centrorhynchidae and Plagiorhynchidae from 21 bird hosts from Paraguay, South America collected between 1982 and 1989.

Host	Host field no. Py	Locality	Dept.	Geographical coordinates	Acanthocephalan
Ciconiiformes: Ardeidae					
<i>Ardea alba</i> Linnaeus, 1758	6609	Transchaco 180	Pte Hayes	-24.05 -58.37	<i>Lueheia inscripta</i> (Westrumb, 1821)
Cuculiformes: Cuculidae					
<i>Crotophaga ani</i> Linnaeus, 1758	2627	Santa Maria	Itapua	-26.99 -55.82	<i>Centrorhynchus guira</i> Lunaschi & Drago, 2010
Falconiformes: Accipitridae					
<i>Buteo magnirostris</i> (Gmelin, 1788)	2169	15 Km E from Cerrito	Paraguari	-26.39 -57.31	<i>Centrorhynchus varius</i> n. sp.
Buteogallus meridionalis (Latham, 1790)					
	6066	Puerto Militar 35	Pte Hayes	-23.52 -57.78	<i>Centrorhynchus varius</i>
	4079	Transchaco 110	Pte Hayes	-24.52 -58.03	<i>Centrorhynchus varius</i>
	4143	Pratts Gill	Boqueron	-22.56 -61.71	<i>Centrorhynchus varius</i>
	6682	Transchaco 293	Pte Hayes	-23.40 -58.99	<i>Centrorhynchus varius</i>
	4902	Transchaco 293	Pte Hayes	-23.40 -58.99	<i>Centrorhynchus varius</i>
<i>Buteogallus urubitinga</i> (Gmelin, 1788)	6589	Transchaco 70	Pte Hayes	-24.81 -57.77	<i>Centrorhynchus varius</i>
<i>Geranoaetus melanoleucus</i> (Vieillot, 1819)	6528	Aquidaban	Concepcion	-23.11 -57.62	<i>Centrorhynchus geranoaeti</i> n. sp.
<i>Parabuteo uncinatus</i> (Temminck, 1824)	6068	Transchaco 115	Pte Hayes	-24.48 -58.05	<i>Centrorhynchus varius</i>
Falconidae					
<i>Herpethores cachinnans</i> (Linnaeus, 1758)	7334	Santa Sofia 10E	Concepcion	-22.33 -57.07	<i>Centrorhynchus</i> sp.
Passeriformes: Furnariidae					
<i>Synallaxis</i> sp.	7250	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Lueheia inscripta</i>
Turdidae					
<i>Turdus amaurochalinus</i> Cabanis, 1850	7372	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Lueheia inscripta</i>
	7373	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Lueheia inscripta</i>
	7373	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Centrorhynchidae</i>
Tyrannidae					
<i>Pitangus sulphuratus</i> (Linnaeus, 1766)	3281	Arroyo Tagatiya-Guazu	Concepcion	-22.76 -57.45	<i>Centrorhynchus pitangi</i> n. sp.
Thamnophilidae					
<i>Taraba major</i> (Vieillot, 1816)	4891	Arroyo Agua-Pey	Itapua	-27.13 -56.28	<i>Centrorhynchus pitangi</i>
	4895	Arroyo Agua-Pey	Itapua	-27.13 -57.28	<i>Centrorhynchus pitangi</i>
Strigiformes: Strigidae					
<i>Megascops choliba</i> (Vieillot, 1817)	7360	S-Lorenzo N 10E	Central	-26.78 -57.49	<i>Lueheia inscripta</i>
	2123	Arroyo Agua-Pey	Itapua	-27.13 -56.28	<i>Centrorhynchus millerae</i> n.sp.
	4886	Arroyo Agua-Pey	Itapua	-27.13 -57.28	<i>Centrorhynchus millerae</i>

TABLE 2. Adults and cystacanths of Acanthocephala, collected from bird hosts in Paraguay, South America between 1982 and 1989, which could not be fully identified.

Host	Host field no. Py	Helminth registration no. INVE	Locality	Department	Geographical coordinates	Notes
Caprimulgiformes: Caprimulgidae						
<i>Caprimulgus parvulus</i> Gould, 1837	4748	38450	Rio Piribebuy	Cordillera	-25.08 -57.35	3 pieces of adult
Cuculiformes: Cuculidae						
<i>Guirra guirra</i> (Gmelin, 1788)	5363	38381	Itaipu	Alto Parana	-25.02 -54.50	cystacanth, proboscis inverted possibly <i>Centrorhynchus</i> sp.
Passeriformes: Dendrocolaptidae						
<i>Campylorhamphus trochilirostris</i> (Lichtenstein, 1820)	7417	38403	S Lorenzo N 10E	Central	-26.78 -54.49	cystacanth, <i>Centrorhynchus</i> sp.
<i>Lepidocolaptes angustirostris</i> (Vieillot, 1819)	2229	38473	Est. Montiel Potrero	Paraguari	-26.39 -57.31	1 cystacanth, probably <i>Centrorhynchus</i> sp.
Emberizidae						
<i>Emberizoides herbicola</i> (Vieillot, 1817)	3487	38438	Tobati	Cordillera	-25.28 -57.09	1 female, no proboscis or proboscis receptacle
Hirundinidae						
<i>Stelgidopteryx ruficollis</i> (Vieillot, 1817)	4273	38458	Rio Guazu, Rte 3	San Pedro Jejuí	-24.10 -56.45	1 female, no proboscis possibly <i>Mediorhynchus</i> sp.
Icteridae						
<i>Chrysomus cyanopus</i> (Vieillot, 1819)	8274	38140	General Diaz	Alto Paraguay	-21.13 -58.52	1 female, no proboscis or proboscis receptacle
Thraupidae						
<i>Oryzoborus angolensis</i> (Linnaeus, 1766)	6899	38396	Arroyo Tapiracuai	San Pedro	-24.60 -56.49	cystacanths, proboscis inverted
Thamnophilidae						
<i>Taraba major</i> (Vieillot, 1816)	4082	38436	Transchaco 293	Pte Hayes	-23.40 -58.99	cystacanths probably <i>Lueheta inscripta</i>
Turdidae						
<i>Turdus amaurochalinus</i> Cabanis, 1850	4813	48453	Pedro P Pena	Boqueron	-22.45 -62.35	no proboscis, probably <i>Lueheta inscripta</i>
Tyrannidae						
<i>Myiarchus tyrannulus</i> (Statius Muller, 1776)	3585	38435	Rte Montania	Boqueron Madrignon 20	-21.97 -59.95	2 females, no proboscis
<i>Tyrannus savana</i> Vieillot, 1808	4200	38441	Rio Guazu, Rte 3	San Pedro Jejuí	-24.10 -56.45	1 female juvenile, no proboscis
Piciformes: Dendrocolaptidae						
<i>Melanerpes cactorum</i> (d'Orbigny, 1840)	8813	38423	Pozo Arias	Pte Hayes	-23.65 -60.10	1 female no proboscis or proboscis receptacle
Trogoniformes: Trogonidae						
<i>Trogon curucui</i> Linnaeus, 1766	8071 8193	38408 38424	Puente Zinho Arroyo Tagatija-mi	Concepcion Concepcion	-22.38 -56.91 -22.69 -57.58	cystacanths, proboscis inverted 2 pieces of adult



FIGS 1-4

Centrorhynchid species. (1) Juvenile female. (2) Posterior end showing female reproductive tract. (3) Female proboscis showing armature. (4) Proboscis hooks, longitudinal row, hooks 3-14, showing true, transitional and spiniform hooks. Scale bars: 1, 1 mm; 2, 3, 100 μ m; 4, 25 μ m.

268, proboscis receptacle 1005 by 282; lemnisci tubular, longer than proboscis receptacle, 1020; reproductive tract 792 long, genital pore subterminal. The proboscis was armed with 20 or 22 rows of 14 hooks, 7 true hooks + 2 transitional hooks + 5 spiniform hooks; true and spiniform hooks with similar blade lengths, hooks 14 shortest in each row. Hook blade lengths in each longitudinal row: hooks 3, 39.6; 4, 33.0; 5, 33.0; 6, 42.9; 7, 42.9; 8, 39.6; 9, 39.6; 10, 42.9; 11, 46.2; 12, 39.6; 13, 36.3; 14, 29.7

The proboscis armatures of these two specimens differed from each other and from any of the species presently known from South America (Petrochenko, 1958; Lunaschi & Drago, 2010). The presence of spines on the anterior trunk of the female specimen does not fit the diagnosis of the genus *Centrorhynchus*, that is: trunk spineless, but does conform to the diagnosis in all other characters. More specimens are needed of both putative species of centrorhynchid however, before complete identifications and descriptions can be prepared.

***Centrorhynchus guira* Lunaschi & Drago, 2010**

Figs 5-12

MATERIAL EXAMINED: MHNG-INVE-38439; one male, pieces of a male and two females from *Crotophaga ani* Linnaeus, 1758, small intestine; Paraguay, Santa Maria, 28.10.1982.

COMMENTS: The proboscis armature of the specimens from *C. ani*, 32 longitudinal rows of 7-8 + 3-5 + 6-7, a total of 16-19 hooks per row, was consistent with that of *C. guira*. The armature of *C. guira* was described as 32 rows of 8-9 + 4 + 6, 18-19 hooks, although study of the photomicrograph, fig. 1b suggests that there are 5 transitional hooks in some rows (Lunaschi & Drago, 2010). The morphology and morphometrics of the specimens from *C. ani*, with the exception of the neck length, were also consistent with those of *C. guira* (see Table 3). The relevant photomicrograph, fig. 1a, given by Lunaschi & Drago (2010), is not clear although careful scrutiny suggests the neck length is more likely to be about 205-255, a measurement consistent with that of the specimens from *C. ani*, than the 30-68 given in the text. Examination of the male specimens in this study suggest that the genital pore is terminal as stated in Lunaschi & Drago (2010). In the photomicrograph fig. 1e (Lunaschi & Drago, 2010), however, the genital pore appears subterminal. In females the posterior end of the trunk is swollen and the genital pore is subterminal. Figures 5-12 are given here for *C. guira* to show the trunk shape and the relative proportions and positions of the internal organs because they were not illustrated in the original description.

The geographical range of *C. guira* has been extended from Argentina to Paraguay and the host range from *Guira guira* (Gmelin, 1788) to *Cryptopgaga ani*, both belonging to the cuckoo family, Cuculidae.

***Centrorhynchus geranoaeti* n. sp.**

Figs 13-19

MATERIAL EXAMINED: MNHG-INVE-82718; holotype, male, from the small intestine of *Geranoeatus melanoleucos* (Gmelin, 1788); Paraguay, Aquidaban, 12.10.1988. – MNHG-INVE-82719; paratype (allotype), female, from the small intestine of *Geranoeatus melanoleucos* (Gmelin, 1788); Paraguay, Aquidaban, 12.10.1988. – MNHG-INVE-38386; paratypes, male, 1 piece male, 2 females, 1 juvenile female, all from the small intestine of *Geranoeatus melanoleucos* (Gmelin, 1788); Paraguay, Aquidaban, 12.10.1988.

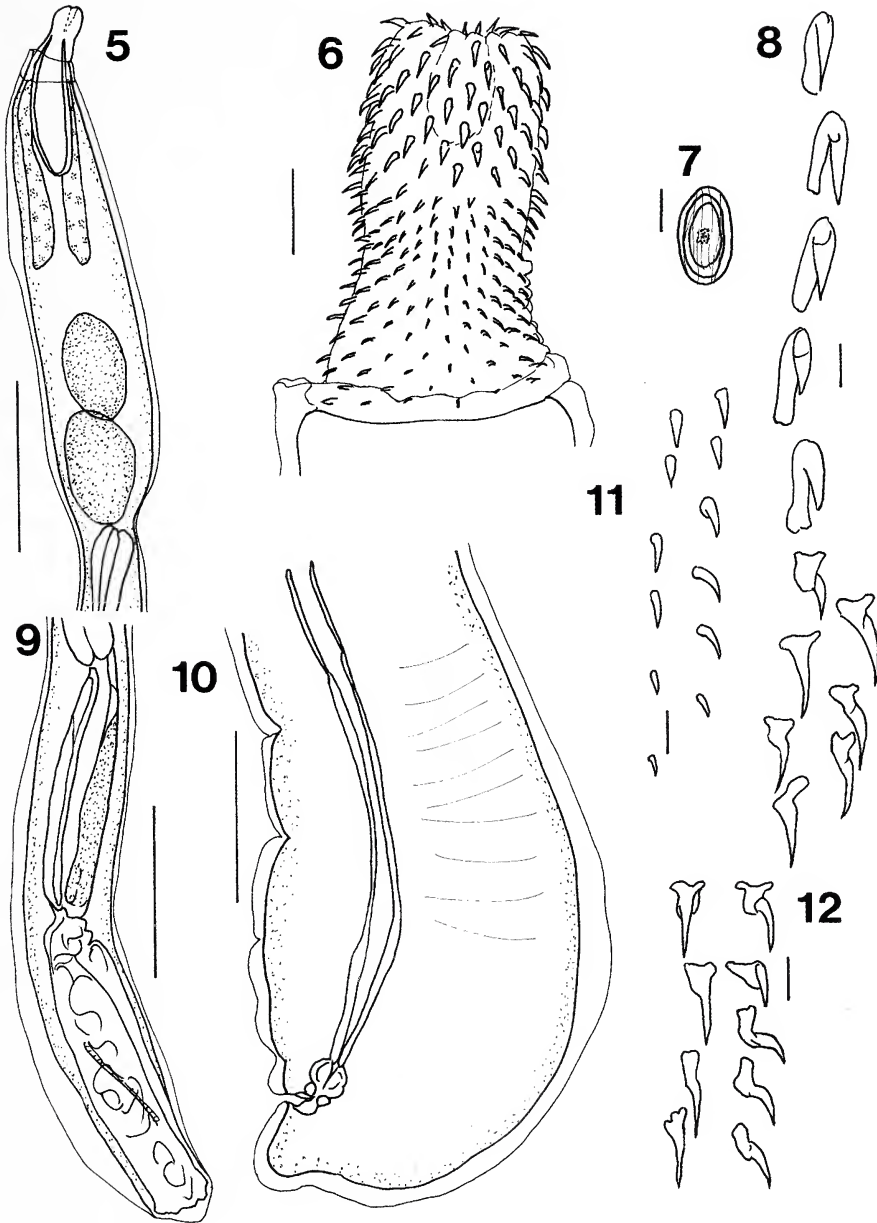
ETYMOLOGY: The species name is taken from the genus name of the host.

DESCRIPTION

General: (based on 2 males, 3 females, and 1 juvenile female) Trunk spineless, elongated; dilated anteriorly in region of testes in male, more or less cylindrical in female terminating in a digitiform process. Neck shorter than broad. Proboscis in 2 parts, slightly wider at base, with constriction anterior to insertion of proboscis receptacle, at about half way between apex and base of proboscis. Proboscis armature 30 rows 20-22 hooks, showing sexual dimorphism. Males: first 7-8 hooks in each longitudinal row with large simple roots, blades hooks 1-6/7 45-50 long, blades hooks 7/8 25 long; next 1-2 hooks with laterally extending shorter roots, blades 10-15 long; posterior 9-11 hooks spiniform, inserted on posterior part of proboscis, blades 10-20 long. Females: first 7-8 hooks with large simple roots, blades 1-7/8, 45-50 long, blades 7/8, 30 long; next 3-4 transitional hooks, blades 25 long; posterior 10-11 hooks spiniform, inserted on posterior part of proboscis, blades 10-30 long. Neck spineless, shorter than broad. Proboscis receptacle double walled. Lemnisci tubular, inserted at

TABLE 3. Comparative measurements of *Centrorhynchus albidus* and selected other species of *Centrorhynchus*, reported from South America, including species from this study; data from Travassos, 1926, Petrochenko, 1958, Schmidt & Neiland, 1966, Lunaschi & Drago, 2010.

	<i>C. albidus</i>	<i>C. geranoeti</i>	<i>C. giganteus</i>	Argentina	<i>C. guira</i>	<i>C. millerae</i>	<i>C. pitangi</i>	<i>C. polymorphus</i>	<i>C. viarius</i>	<i>C. tumidulus</i>
Males			young male	Paraguay						
Trunk length mm	12	15	12.5	26.1-30.9	30	13	9-11	6.5	12-18	15-24
Proboscis length	928-1250	1005	1870	790-970	805	650	1005-1020	670-880	804-1020	
Neck length	18	235		30-68	235-360	221	268-402		268-306	
width	372	636		410-510	470-510	370	670-735		382-510	
Proboscis receptacle length	1160-1250	1410		1400-1600	1200	1200	1307-1360	800-1000	1105-1785	1000-1160
Lemnisci length	1460-2500	1360	5200	1940-2340	2211	1250	2800	1200-2000	1540	1300-2300
Anterior testis length	1000-568	502	300	1060-1200	1088	536	1105-1700	250	470-480	570
width	278	402	250	540-630	476-595	402	476-731	200	248-425	670
Posterior testis length		670		1110-1290	1139-1156	536	1105-1870		603-1190	
width		335	7.0	514-660	527-697	375	510-782		235-425	
Cement glands length mm		6.7			18.0-18.7	8.8	5.1	2.5-3.0	4.3-5.6	10.0-14.0
Saeffigen's pouch length		1400	1000	2710-2970	2380-3400	1300	1200	1000	918-2210	1100-2300
Females			mature female							
Trunk length mm	16	21-22	37-55	38.8-50.4	50-55	25-35	16-19	9	12-35	15-37
Reproductive tract length		1206		2630	2145	900-2250	2000		972-1340	
Proboscis length	1250	1105-1240		920-1000	805	850-900	804-1020		740-1072	
Proboscis receptacle length	1250	1530-1700		1690-1770	1700	1226-1810	1394-1615		1206-1581	
Lemnisci length	2500			1800-2710	2211	1445-1700	2200		1005-1335	
Egg length	42	49.5-56.0	56.0	53-64	46-53	49.5-56.0	56-66.5	44-50	42.5-49.5	53-56
width	20	23-29.5	28-32	24-29	23-30	23.0-29.5	26.5-32.5	22-30	18.5-23.0	21



FIGS 5-12

Centrorhynchus guira Lunaschi & Drago, 2010. (5) Male anterior end. (6) Male proboscis showing armature. (7) Egg. (8) Male proboscis hooks, showing part of longitudinal row of true hooks numbers 4, 5, 6, 7 and 8 and 2 rows of 3 transitional hooks numbers 9, 10, 11 and 9, 10, 11, 12 respectively. (9) Male posterior end. (10) Female posterior end showing bulbous shape and reproductive tract. (11) Male proboscis hooks showing longitudinal rows of 6 spiniform hooks. (12) Female proboscis, longitudinal rows of 4 and 5 transitional hooks showing manubria from differing orientations. Scale bars: 5, 9, 10, 1 mm; 6, 100 μ m; 7, 8, 11, 12, 25 μ m.

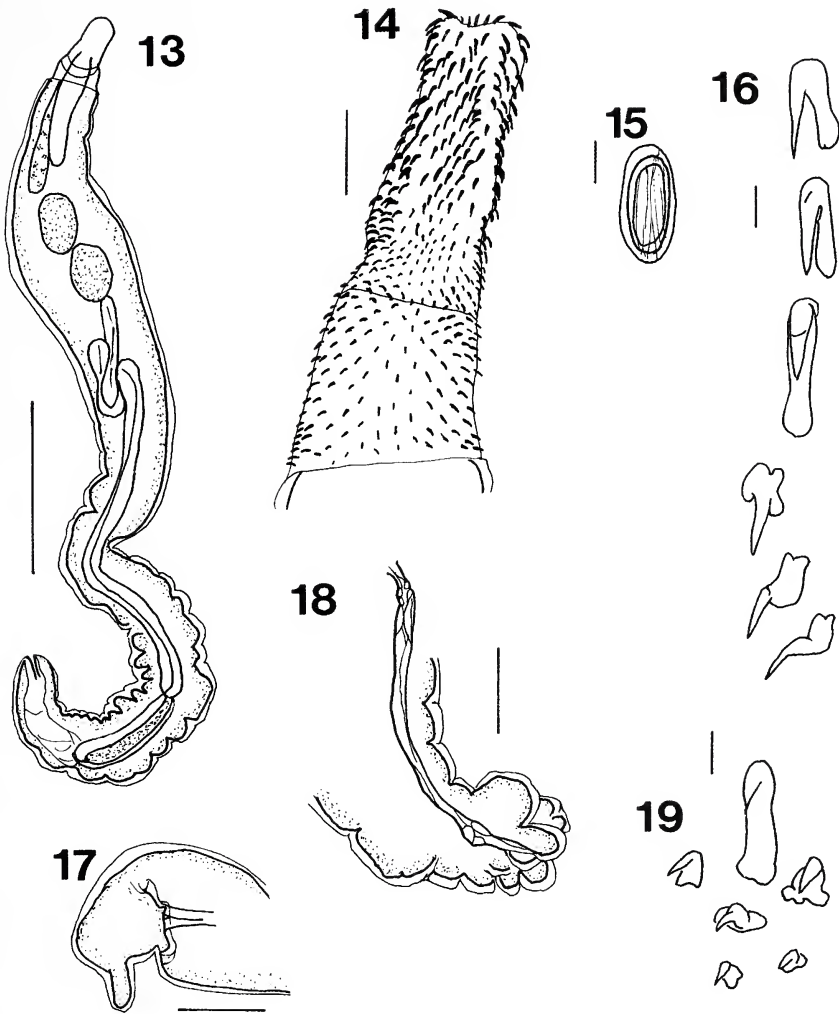
base of neck, extend posteriorly beyond proboscis receptacle. Cerebral ganglion located at mid region of proboscis receptacle, posterior to neck.

Male: (based on 2 specimens) Trunk 15 mm long, 1550 at widest part. Proboscis 1005 long, 335 wide. Neck 235 long, 635 wide at base. Proboscis receptacle 1410 long, 340 wide; lemnisci 1360 long. Testes oval, tandem, not contiguous, in anterior third of trunk; anterior testis 502 long, 402 wide; posterior testis 670 long, 335 wide. Cement glands, 3, elongated, tubular, begin immediately posterior to end of posterior testis, 6700 long; Saeffigen's pouch 1400 long. Genital pore terminal. Entire male system occupies about 88% trunk length.

Female: (Based on 3 specimens) Trunk 21, 22 mm long, 765, 940 wide. Proboscis 1105, 1240 long, 302, 425 wide. Neck 155, 235 long, 535, 605 wide at base. Proboscis receptacle 1530, 1700 long, 255, 325 wide. Lemnisci concealed by eggs. Reproductive tract, uterine bell to genital pore, 1206 long. Posterior end with digitiform papilla, genital pore subterminal. Eggs oval, external shell thick, ridged, 49.5-56.0 (52.8) long, 23.0-29.5 (25.6) wide.

COMMENTS: *Centrorhynchus geranoaeti* n. sp. conforms to the diagnosis of the genus given by Golvan (1956, 1960). *Centrorhynchus geranoaeti* differs from all other species of *Centrorhynchus* in that the female has typical transitional hooks with anteriorly extending manubria but the male does not. In males the anterior true hooks have large simple roots and the posterior ones short laterally extending roots. In the key to the Neotropical species of *Centrorhynchus* by Lunaschi & Drago (2010) *C. geranoaeti* with 30 longitudinal rows of 22-24 hooks, the transitionals with lateral alate processes, falls closest to *C. guira*, with 32 rows of 18-19 hooks, also with transitionals with lateral alate processes. *Centrorhynchus geranoaeti* can be further differentiated from *C. guira*, in having fewer, smaller, transitional hooks (2-3, 10-20 long, compared with 4-5, 19-33 long) and more spiniform hooks (9-11 compared with 6-7) in each longitudinal row. *Centrorhynchus geranoaeti* is a smaller worm than *C. guira*, with a longer proboscis, lemnisci not extending posteriorly beyond the proboscis receptacle, smaller testes, shorter cement glands, Saeffigen's pouch and female reproductive tract. The female trunk is more or less cylindrical, terminating in a digitiform process in *C. geranoaeti* and swollen posteriorly in *C. guira*. See Table 3 for comparative measurements.

Centrorhynchus geranoaeti with a proboscis armature of 30 rows of 22-24 hooks per row is also near to *C. albidus* and *C. polymorphus*, both having 28-30 rows of hooks and nearest to *C. albidus* that has 20-22 hooks per row (Schmidt & Neiland, 1966). Lunaschi & Drago (2010) interpret the proboscis armature of *C. albidus*, from figure 5 of Schmidt & Neiland (1966), as being up to 30 rows of 8 + 4 + 10 hooks per row. The descriptive text states "first 7 hooks in each row with well developed root, next hook with reduced root, next 13 or 14 hooks rootless" (Schmidt & Neiland, 1966). A careful study of figure 5, however, shows 8 hooks with true roots, the next with a reduced root and manubrium, then 3 with manubrium only and the last 10 rootless spines. Using this latter interpretation *C. geranoaeti* and *C. albidus* further differ in the number and form of each type of hook in each row (for males 8-10 hooks with large roots + 1-2 hooks with reduced roots + 9-10 spiniform hooks, compared with 7-8 hooks



FIGS 13-19

Centrorhynchus geranoaeti sp. n. (13) Male. (14) Female proboscis, showing armature. (15) Egg. (16) Female proboscis hooks, longitudinal row showing true hooks 8, 9, 10 and 3 transitional hooks. (17) Female posterior end. (18) Female posterior end showing reproductive tract, trunk contracted, posterior digitiform process inverted. (19) Male proboscis hooks, showing examples of a true hook with a large simple root and true hooks with reduced roots. Scale bars: 13, 1 mm; 14, 200 μ m; 15, 16, 19, 25 μ m; 17, 500 μ m; 18, 400 μ m.

with large roots + 1 hook with reduced root and manubrium + 3 transitional hooks + 9-11 spiniform hooks). *Centrorhynchus geranoaeti* has smaller testes and larger eggs than *C. albidus* (Table 3).

Centrorhynchus geranoaeti further differs from *C. polymorphus* in the number of hooks per row (22-24 compared with 17), body shape (cylindrical not claviform)

and length of proboscis, proboscis receptacle, cement glands and testis size (Table 3). Dimitrova & Gibson (2005) suggested that shape and size of the body and proboscis of *C. polymorphus* better fits the generic diagnosis of *Sphaerirostris* than of *Centrorhynchus* (see Golvan, 1956, 1960).

Centrorhynchus simplex Meyer, 1932, from Brazil was described only from juvenile forms encysted in the body cavity of a snake. The identity of the host is uncertain although the name given in the text, *Coluber olivaceus*, may be *Liophis poecilogyrus* (Wied-Neuwied, 1825). *Centrorhynchus simplex* can be distinguished from *C. geranoaeti* by the proboscis armature of 22-24 longitudinal rows of 24 hooks (Petrochenko, 1958).

Six species of *Centrorhynchus* are found in North America (Richardson & Nickol, 1995). *Centrorhynchus kuntzi* has also been recorded from Nicaragua and *C. microcephalus* from Mexico, both therefore being included in the key to the Neotropical species of *Centrorhynchus*. Of the remaining four species, *C. californicus* Millzner, 1924, *C. conspectus* Van Cleave & Pratt, 1940 and *C. robustus* Richardson & Nickol, 1995 have been reported only from the United States of America (Richardson & Nickol, 1995) and *C. spinosus* (Kaiser, 1893) from the United States and the Galapagos Islands (Van Cleave, 1924, 1940; Richardson & Nickol, 1995). *Centrorhynchus californicus*, *C. conspectus* and *C. robustus* can be distinguished from *C. geranoaeti* by their proboscis armature, having neither 30 longitudinal rows of hooks nor 10-12 true hooks, nor any transitional hooks in either male or female in each longitudinal row. *Centrorhynchus spinosus* is a larger worm than *C. geranoaeti* (male 30-45 mm compared with 15 mm), although with 32 rows of hooks it has a similar proboscis armature. However *C. spinosus* has no transitional hooks in either male or female and more spiniform hooks than *C. geranoaeti* (14-15 compared with 9-11) per row and the hooks of *C. spinosus* are larger than those of *C. geranoaeti* (48-60 compared with 10-50).

***Centrorhynchus millerae* sp. n.**

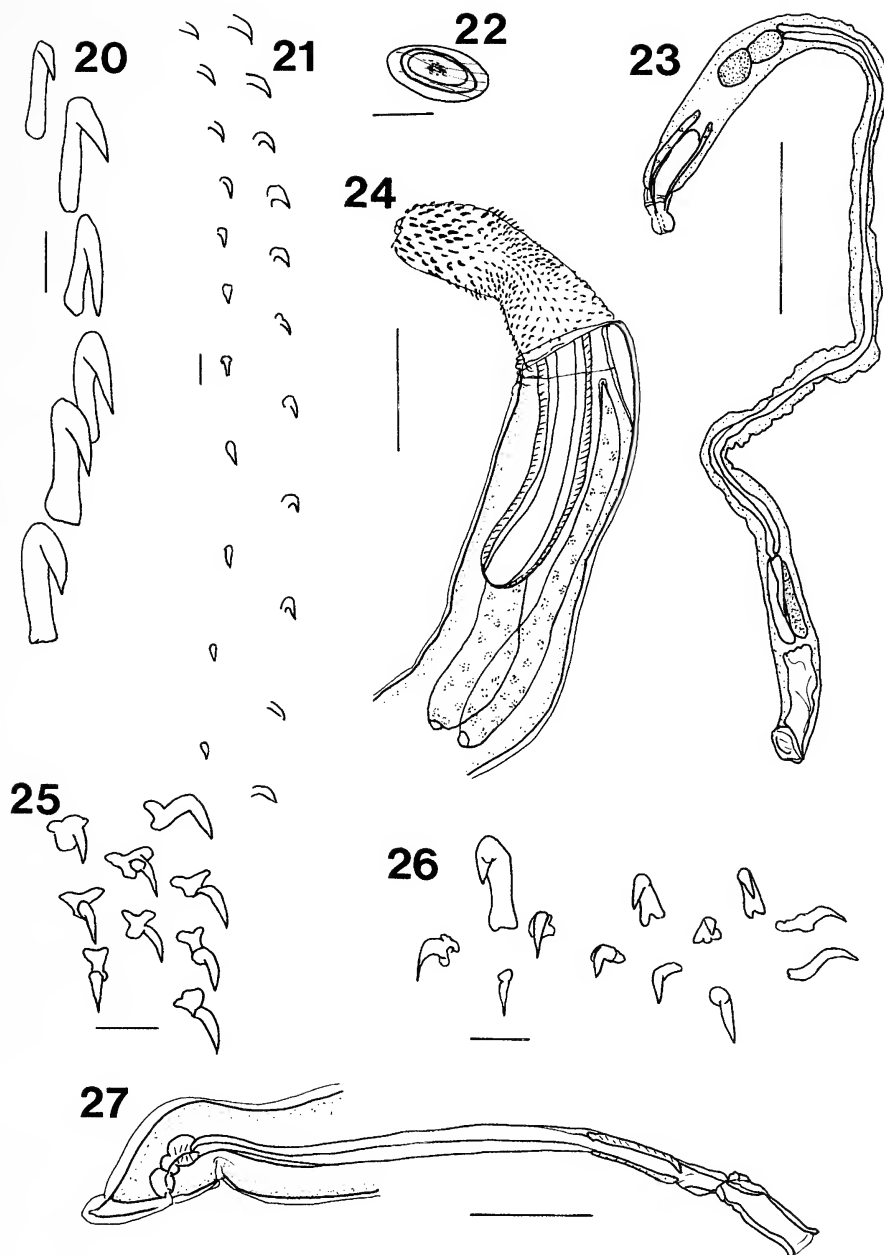
Figs 20-27

MATERIAL EXAMINED: MNHG-INVE-82720; holotype, male, from *Megascops choliba* (Vieillot, 1817), small intestine: Paraguay, Arroyo Agua-Pey, 25.10.1986. – MNHG-INVE-82721; paratype (allotype) female, from *Megascops choliba* (Vieillot, 1817), small intestine: Paraguay, Arroyo Agua-Pey, 25.10.1986. – MNHG-INVE-38444, paratypes 3 pieces female from *Megascops choliba* (Vieillot, 1817), small intestine: Paraguay, Arroyo Agua-Pey, 25.10.1986. – MNHG-INVE-38443; voucher specimens, 4 females, 6 pieces female from *M. choliba*, small intestine: Paraguay, Arroyo Agua-Pey, 10.10.1982.

ETYMOLOGY: This species is named in honour of the Director of the South Australian Museum.

DESCRIPTION

General: (based on 1 male, 5 females, and 6 pieces of females) Trunk spineless, elongated; dilated anteriorly in region of testes in male, with swollen posterior end terminating in digitiform process in female. Neck shorter than broad. Proboscis in 2 parts, widest at base, with constriction at insertion of proboscis receptacle about 60% of distance from apex to proboscis base, anterior proboscis slightly expanded anterior to constriction. Proboscis armature 30-32 longitudinal rows 17-20 hooks, showing sexual



FIGS 20-27

Centrorhynchus millerae sp. n. (20) Female proboscis hooks, longitudinal row true hooks 1-6. (21) Female proboscis hooks, longitudinal row 11 spiniform hooks. (22) Egg. (23) Male. (24) Female, anterior end. (25) Female proboscis hooks, longitudinal rows 2-3 transitional hooks. (26) Male proboscis hooks, showing true hooks with simple roots and 1-2 hooks with reduced roots. (27) Female reproductive tract. Scale bars: 20, 22, 25, 26, 25 μm ; 21, 12.5 μm ; 23, 1 mm; 24, 27, 400 μm .

dimorphism. Male: in each longitudinal row first 5-6 hooks with large simple roots, blades 20-50 long, blades hooks 3, 45-50, longest, blades hooks 1, 6, 20-30, shortest; next hook with reduced root, blade 18-20 long, next 10-14 hooks spiniform, blades 11-15 long. Female: in each longitudinal row first 5-6 hooks with large simple roots, blades hooks 3 longest, blades hooks 1, 6 shortest; 3-4 transitional hooks with manubria, blades 20-25 long; next 9-12 hooks spiniform, blades 10-15 long, inserted on posterior part of proboscis. Neck spineless, shorter than broad. Proboscis receptacle double walled. Lemnisci elongated, claviform, inserted at base of neck, extend posteriorly beyond proboscis receptacle. Cerebral ganglion located at mid region of proboscis receptacle, posterior to neck.

Male: (based one specimen) Trunk 13 mm long, 1700 at widest part. Proboscis partly inverted estimated length 650, width 302. Neck 221 long, 370 wide at base. Proboscis receptacle 1200 long, 308 wide; lemnisci 1250 long. Testes oval, tandem, contiguous, in anterior third of trunk; anterior testis 536 long, 402 wide; posterior testis 536 long, 375 wide. Cement glands, 3 or 4 (number not determined), elongated, tubular, begin immediately posterior to end of posterior testis, 8800 long; Saeftigen's pouch 1300 long. Genital pore terminal. Entire male system occupies about 80% trunk length.

Female: (Based on 5 specimens) trunk 25-35 (29.5) mm long, 470-590 (575) wide. Proboscis 850-900 (875) long, 280-320 (299) wide. Neck 155-270 (203) long, 402-435 (420) wide at base. Proboscis receptacle 1226-1810 (1409) long, 205-340 (267) wide. Lemnisci 1445-1700 (1509) long. Reproductive tract, uterine bell to genital pore, 900-2250 (1575) long. Genital pore subterminal. Eggs oval, external shell thick, ridged, 49.5-56.0 (53.1) long, 23.0-29.5 (26.7) wide.

COMMENTS: *Centrorhynchus millerae* sp. n. conforms to the diagnosis of the genus given by Golvan (1956, 1960). *Centrorhynchus millerae* differs from all species of *Centrorhynchus*, except *C. geranoaeti*, in that only the females have a proboscis armature with transitional hooks. *Centrorhynchus millerae* differs from *C. geranoaeti* in the number hooks per row (16-20, of which 5-7 are true hooks compared with 22-24, 8-12) and the form of the transitional hooks, with lateral alate processes on the manubria for *C. millerae*, without for *C. geranoaeti*. *Centrorhynchus millerae* has a shorter proboscis and longer cement glands than *C. geranoaeti* (Table 3). *Centrorhynchus millerae* occurs in the passerine, *Pitangus sulfuratus*, the great kiskadee and *C. geranoaeti* in the strigiform, *Megascops cholida*, the tropical screech owl.

In the key to the Neotropical species of *Centrorhynchus* (Lunaschi & Drago, 2010) *C. millerae*, clusters together with *C. guira* and *C. kuntzi* as a third species with lateral alate processes on the transitional hooks. *Centrorhynchus millerae* is closest to, but differs from, *C. guira* in the number and arrangement of hooks of the proboscis armature (30-32 rows of 16-20 hooks compared with 32 rows of 16-19 hooks). *Centrorhynchus millerae* further differs from *C. guira* in having fewer true hooks and more spiniform hooks per row (5-6 and 9-14 compared with 7-9 and 6-7). *Centrorhynchus millerae* is a smaller worm than *C. guira* and has shorter lemnisci, smaller testes, shorter cement glands and shorter female reproductive tract (Table 3).

Centrorhynchus simplex, also from South America, and each of the species of *Centrorhynchus* from North America, as discussed above for *C. geranoaeti*, can be

further distinguished from *C. millerae* by their proboscis armature, having differing combinations of true and spiniform hooks and no transitional hooks.

***Centrorhynchus pitangi* n. sp.**

Figs 28-37

MATERIAL EXAMINED: MNHG-INVE-82722; holotype male from *Pitangus sulfuratus* (Linnaeus, 1776), small intestine: Paraguay, Arroyo Agua-Pey, 26.10.1986. – MNHG-INVE-82723; paratype (allotype) female from *Pitangus sulfuratus* (Linnaeus, 1776), small intestine: Paraguay, Arroyo Agua-Pey, 26.10.1986. – MNHG-INVE-38406; paratypes, from *Pitangus sulfuratus* (Linnaeus, 1776), small intestine: Paraguay, Arroyo Agua-Pey, 26.10.1986. – MNHG-INVE-38448; voucher specimens, 1 female, from *Pitangus sulfuratus* (Linnaeus, 1776), small intestine: Paraguay, Arroyo Agua-Pey, 26.10.1986. – MNHG-INVE-38447; 1 juvenile, from *P. sulfuratus* small intestine: Paraguay, Arroyo Tagatiya- Guiazu 17.10. 1983.

ETYMOLOGY: The species name is taken from the genus name of the host.

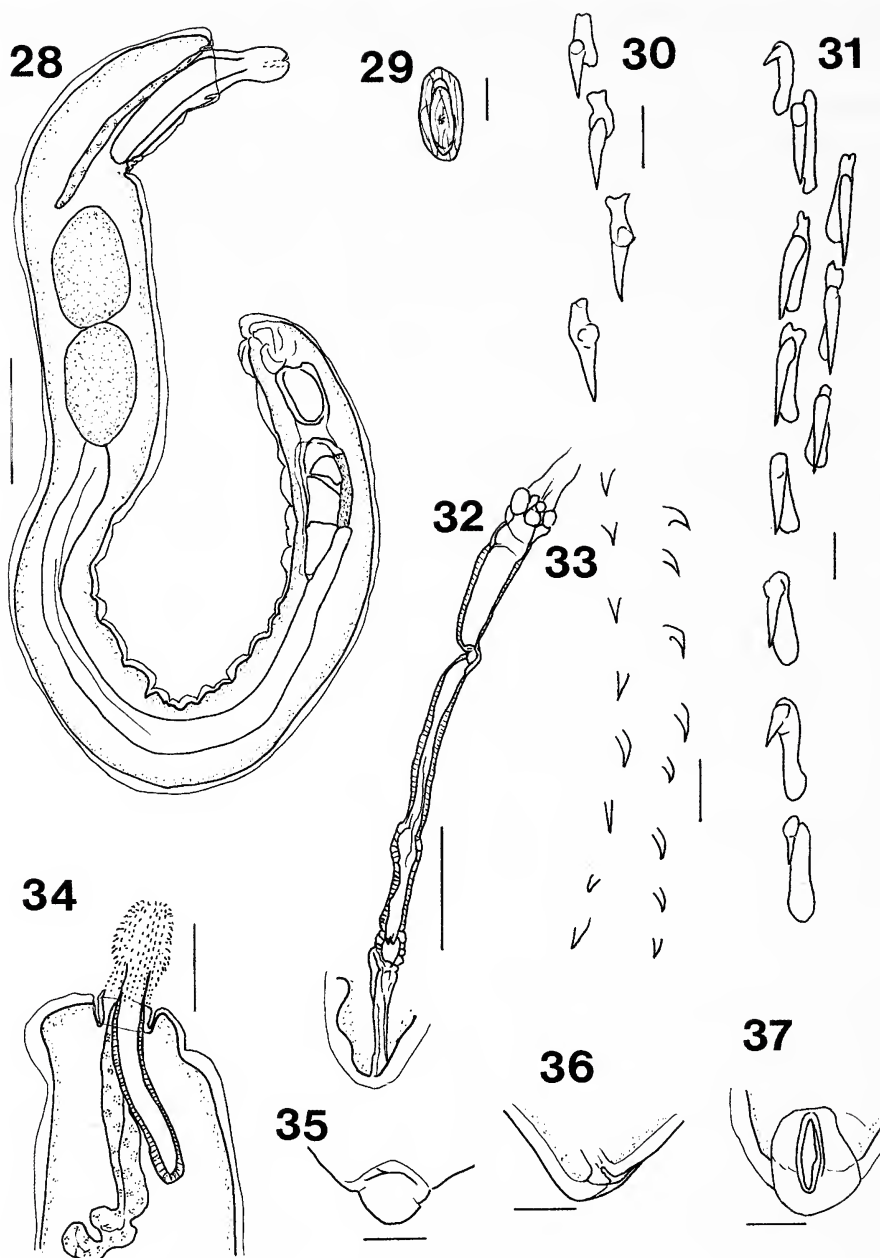
DESCRIPTION

General: (based on 2 males, pieces of 2 males, 5 females, and pieces of 5 females) Trunk spineless, elongated; more or less cylindrical in female, dilated anteriorly in region of testes in male. Neck shorter than broad. Proboscis in 2 parts, with constriction at insertion of proboscis receptacle, at about 62% of distance from apex to proboscis base, anterior proboscis slightly expanded above constriction. Proboscis armed with 28-30 longitudinal rows 18-20 hooks. Anterior 7-8 hooks with large simple roots, first 4 also with manubria, blades hooks 1, 13.2, 39.6 long, hooks 2, 46.2, 49.5 long, hooks 3, 42.9 long, hooks 4, 39.6, 42.9 long, hooks 5, 36.3-39.6 long, hooks 6, 33- 36.3 long, hooks 7, 33 long, hooks 8, 26.4, 29.7 long; next hook with reduced root and manubrium, blade 27 long; following 3 transitional hooks with manubria, blades 33-39.5 long; posterior 7-8 hooks spiniform, blades 10-30 long, inserted on posterior part of proboscis. Neck spineless, shorter than broad. Proboscis receptacle double walled. Lemnisci tubular, inserted at base of neck, extend posteriorly beyond proboscis receptacle. Cerebral ganglion located at mid region of proboscis receptacle, posterior to neck.

Male: (based on two specimens) Trunk 9, 11 mm long, 1360 at widest part. Proboscis 1005, 1020 long, 280, 301 wide. Neck 268, 402 long, 670, 735 wide at base. Proboscis receptacle 1360, 1307 long, 201-306 wide; lemnisci 2800 long. Testes oval, tandem, contiguous, in anterior third of trunk; anterior testis 1700, 1105 long, 476, 731 wide; posterior testis 1870, 1105 long, 510, 782 wide. Cement glands, 3, elongated, tubular, begin immediately posterior to end of posterior testis, 5100 long; Saeftigen's pouch 1200 long. Genital pore subterminal. Entire male system occupies about 85% trunk length.

Female: (Based on 5 specimens) Trunk 16-19 (18) mm long, 1190-1615 (1465) wide. Proboscis 804-1020 (946) long, 301-368 (320) wide. Neck 335-402 (370) long, 470-670 (570) wide at base. Proboscis receptacle 1394-1615 (1495) long, 238-295 (252) wide. Lemnisci 2200 long. Reproductive tract, uterine bell to genital pore, 2000 long. Genital pore subterminal. Eggs oval, external shell thick, ridged, 56.0-66.3 (58.8) long, 26.4-32.3 (27.9) wide.

COMMENTS: *Centrorhynchus pitangi* sp. n. conforms to the diagnosis of the genus given by Golvan (1956, 1960). In the key to the Neotropical species of



FIGS 28-37

Centrorhynchus pitangi sp. n. (28) Male. (29) Egg. (30) Proboscis hooks, longitudinal row 4 transitional hooks. (31) Proboscis hooks, longitudinal row true hooks 1-8, 4 with manubria. (32) Female genital tract, dissection. (33) Proboscis hooks, longitudinal rows 8 spiniform hooks. (34) Female anterior end. (35) Female posterior tip of trunk, ventral view. (36) Female posterior tip of trunk, lateral view. (37) Male posterior tip of trunk, bursa inverted, ventral view. Scale bars: 28, 32, 1 mm; 29, 30, 31, 33, 25 μ m; 34, 500 μ m; 35, 36, 37, 100 μ m.

Centrorhynchus by Lunaschi & Drago (2010) *C. pitangi* falls close to *C. giganteus* Travassos, 1926 in the form of the true hooks, both species having true hooks with manubria as well as transitional hooks with manubria. The two species differ in proboscis armature *C. pitangi* having 28-30 longitudinal rows of 18-20 hooks compared with 24-26 rows of 27-28 hooks for *C. giganteus*. Further the blades of the true hooks of *C. pitangi* are shorter than those of *C. giganteus* (13.5-43 compared with 100-150). Travassos (1926) does not use the term transitional hooks to describe hooks with manubria but no roots, separating the hooks only into 16-17 hooks and 11 spines in each row. His plate 9, figure 22, of hook types, however, shows at least one spine in each row was a transitional type, with manubrium and without a root. Therefore in comparing numbers of hook types in this instance, transitional hooks should be counted as true hooks. Accordingly *C. pitangi* would have 11-12 hooks and 7-8 spines compared with 16-17 hooks and 7-8 spines for *C. giganteus*. *Centrorhynchus pitangi* can be further distinguished from *C. giganteus* as a smaller worm (females 16-19 compared with 37-55mm long) with a shorter proboscis (up to 1020 long, compared with 1870), shorter lemnisci (2200-2800 compared with 5200 long) and smaller testes (up to 1870 compared with 3000 long) (Travassos, 1926).

Although not recognized by Lunaschi & Drago (2010) *C. tumidulus*, as described and figured by Travassos (1926, see p. 68 and fig. 5) also has true hooks with manubria. *Centrorhynchus pitangi* can be distinguished from *C. tumidulus* by the number of hooks of the proboscis armature (28-30 rows of 18-20 hooks compared with 26 rows of 20-21 hooks) and in having transitional hooks which *C. tumidulus* lacks. Further *C. pitangi* is a smaller worm with larger testes, longer lemnisci, shorter cement glands and larger eggs than *C. tumidulus* (Table 3).

Centrorhynchus albidus and *C. polymorphus* are the other species from South America having a proboscis armature of up to 30 longitudinal rows of hooks (Lunaschi & Drago, 2010). *Centrorhynchus pitangi* differs from both species in form of the true hooks. *Centrorhynchus pitangi* further differs from *C. albidus* in the total number of hooks per row (18-20 compared with 20-22 hooks) and the numbers of each type of hook, as interpreted above (7-8 true hooks, 4 with manubria + 1-2 true hooks with reduced root and manubrium + 2-3 transitional hooks + 7-8 spiniform hooks compared with 7-8 true hooks + 1 hook with reduced root and manubrium + 3 transitional hooks + 10-11 spiniform hooks) (Schmidt & Neiland, 1966). *Centrorhynchus pitangi* has larger testes and larger eggs than *C. albidus* (Table 3).

Centrorhynchus pitangi further differs from *C. polymorphus* in proboscis armature, the total number of hooks per row (18-20 compared with 17) and the number of each type of hook in each row (8-9 including true hooks with manubria + 2-3 + 7-8 compared with 7+3+7) (Travassos, 1926), as well as in body length and shape, cylindrical not claviform, the length of the proboscis, proboscis receptacle, cement glands and Saeffigen's pouch and the size of the testes and eggs (Table 3).

Centrorhynchus pitangi differs from all other species found in Paraguay, *C. guira*, *C. geranoaeti* and *C. millerae* in proboscis armature, both in the morphology and the numbers of true hooks and spines. *Centrorhynchus guira* has 32 rows of 18-19 hooks, 4 being transitional hooks with lateral alate processes and 6 spiniform hooks. *Centrorhynchus geranoaeti* and *C. millerae* have females with and males without

transitional hooks in 30, 30-32 rows of 22-24 and 16-20 hooks including 9-11 and 9-14 spiniform hooks respectively.

Centrorhynchus pitangi can be distinguished from *C. opimus* by the number of longitudinal rows of proboscis hooks (28-30 compared with 24) and by having true hooks 8-9 with reduced roots and manubria. Travassos (fig. 27, plate 11, 1926) shows anterior true hooks with manubria and transitional hooks but not hooks with reduced roots and manubria. *Centrorhynchus pitangi* has a shorter trunk (9-11 compared with 12-16 for males) longer lemnisci (2200-2800 compared with 2000) and longer cement glands (5100 compared with 2700) than *C. opimus*.

Centrorhynchus simplex, found in Brazil, can be distinguished from *C. pitangi* by the proboscis armature. Similarly *C. pitangi* can be differentiated from each of the four species of *Centrorhynchus* found only in North America by a combination of the characters of the proboscis armature; numbers, arrangement, morphology and sizes of hooks as detailed for *C. geranoaeti* above.

Centrorhynchus viarius n. sp.

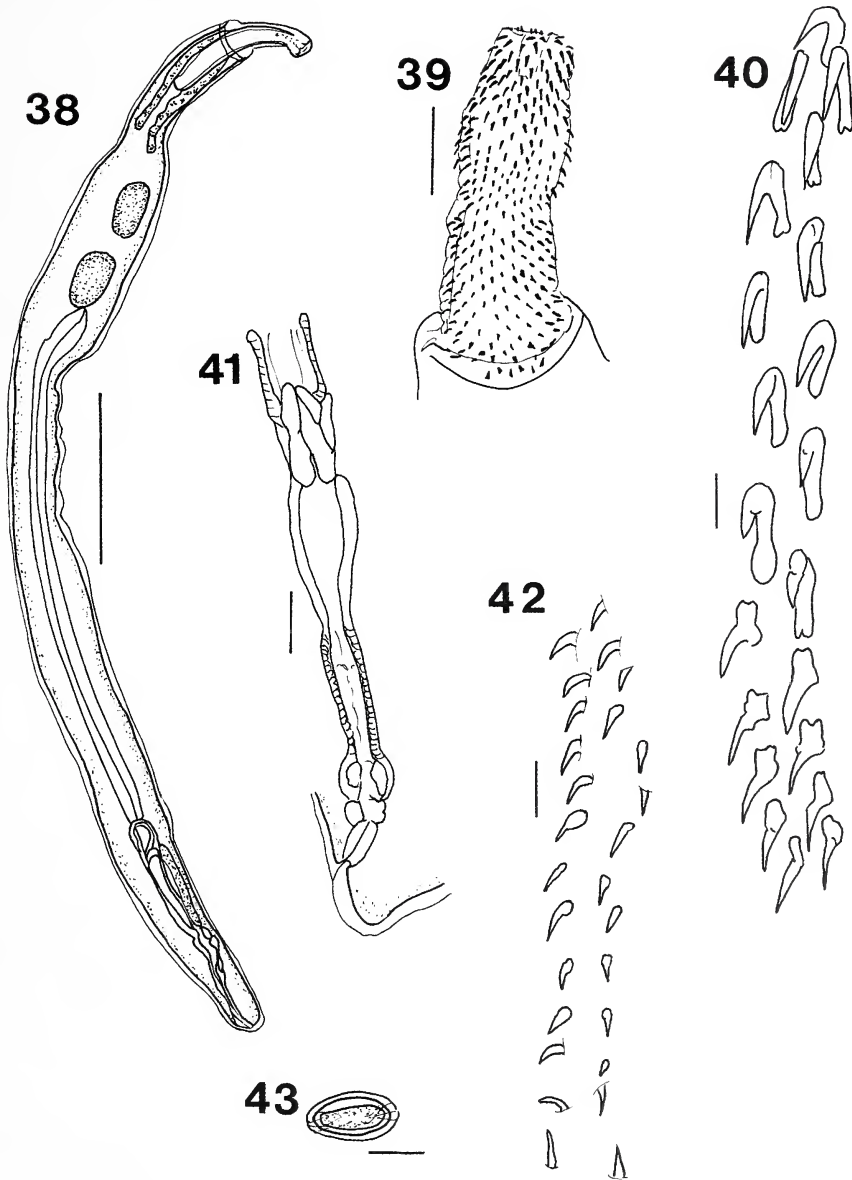
Figs 38-43

MATERIAL EXAMINED: MHNG-INVE-82724; holotype, male, from *Buteogallus meridionalis* (Latham, 1790), small intestine; Paraguay, Transchaco 293, Pte Hayes; 04.11.1983. – MHNG-INVE-82725, paratype (allotype), female, from *Buteogallus meridionalis* (Latham, 1790), small intestine; Paraguay, Transchaco 293, Pte Hayes; 04.11.1983. – MHNG-INVE-38393; paratypes from *Buteogallus meridionalis* (Latham, 1790), small intestine; Paraguay, Transchaco 293, Pte Hayes; 04.11.1983. – MHNG-INVE-38455, voucher specimens, 1 female, from *Buteogallus meridionalis* (Latham, 1790), small intestine; Paraguay, Transchaco 293, Pte Hayes; 05.07.1985. – MNHG-INVE-38459, 38456, 38457, 383843, juvenile males, pieces of males, 5 females, pieces of females from *Buteo magnirostris* (Gmelin, 1788), small intestine; Paraguay, Transchaco 95, 110, 15 km E from Cerrito, Pratts Gill, 12.10.1982, 01.08.1951995, 01. 07.1995, 07.11.1987. – MHNG-INVE-38388, 1 female from *Buteogallus urubitinga* (Gmelin, 1788), small intestine; Paraguay, Transchaco 70, 24.10.1988. – MNHG-INVE-38385, 1 male, 5 pieces female from *Parabuteo uncinatus* (Temminck, 1824), small intestine; Paraguay, Transchaco 115, 07.11.1987.

ETYMOLOGY: The species name is taken from *viari*, of the roadside, and refers to the fact that all the hosts were collected from along the Transchaco.

DESCRIPTION

General: (based on 5 males, 3 juvenile males, 14 pieces of male, 12 females and 35 pieces of female) Trunk spineless, elongated, more or less cylindrical, dilated anteriorly in region of testes. Neck shorter than broad. Proboscis in 2 parts, with constriction at insertion of proboscis receptacle at about 50% of distance from apex to proboscis base; anterior proboscis slightly expanded above constriction. Proboscis armed with 28-30 rows 23-27 hooks, lengths of hook blades vary irregularly along each row, longest blades usually hooks 3-5, shortest blades, usually hooks 19-22. Anterior 8-9 hooks with large simple roots, blades hooks 2, 35 long, hooks 3, 32, 38 long, hooks 4, 38, 40 long, hooks 5, 20-40 long, hooks 6, 35-40 long, hooks 7, 30-40 long, hooks 8, 20-32 long, hooks 9, 25 long; next 4-5 hooks transitional, blades 18-30 long; posterior 12-13 hooks spiniform, inserted on posterior part of proboscis, longest blades last 2 hooks in row, 10-30 long. Neck spineless, shorter than broad. Proboscis receptacle double walled. Lemnisci tubular, inserted at base of neck, extend posteriorly



FIGS 38-43

Centrorhynchus viarius sp. n. (38) Male. (39) Male proboscis, showing armature. (40) Proboscis hooks, longitudinal rows of true hooks 3-7, 2-8, and transitional hooks 5, 4. (41) Female reproductive tract. (42) Proboscis hooks, longitudinal rows of spiniform hooks 13, 14. (43) Egg. Scale bars: 38, 1 mm; 39, 200 μm; 40, 42, 43 25 μm; 41, 100 μm.

beyond proboscis receptacle. Cerebral ganglion located at mid region of proboscis receptacle, posterior to neck.

Male: (Based on 5 specimens) Trunk 12-18 (14) mm long, 490-835 (693) wide. Proboscis 805-1020 (871) long, 268-306 (298) wide. Neck 268-340 (315) long, 382-510 (470) wide at base. Proboscis receptacle 1105-1785 (1334) long, 181-290 (220) wide; lemnisci (single measurement) 1540 long. Testes oval, tandem, not contiguous, in anterior third of trunk; anterior testis 470-840 (727) long, 248-425 (296) wide; posterior testis 603-1190 (828) long, 235-425 (344) wide. Cement glands, 4, elongated, tubular, begin immediately posterior to end of posterior testis, 4335-5610 (4972) long; Saeftigen's pouch 918-2210 (1309) long. Genital pore terminal. Entire male system occupies about 85-90% of trunk length.

Female: (Based on 7 specimens) trunk 12-35 (19) mm long, 510-1020 (755) wide. Proboscis 740-1072 (871) long, 268-335 (306) wide. Neck 201-536 (358) long, 402-570 (486) wide at base. Proboscis receptacle 1206-1581 (1407) long, 227-325 (267) wide. Reproductive tract, uterine bell to genital pore, 972-1340 (1184). Genital pore subterminal. Eggs oval, external shell thick, ridged, 42.5-49.5 (46.0) long, 18.5-23.0 (21.5) wide.

COMMENTS: *Centrorhynchus viarius* sp. n. conforms to the diagnosis of the genus given by Golvan (1956, 1960). In the key to the Neotropical species of *Centrorhynchus* of Lunaschi & Drago (2010) *C. viarius* falls within the group of species with a proboscis armature which has transitional hooks without lateral alate processes, namely *C. albidus*, *C. polymorphus*, *C. crotophagicola* and *C. microcephalus*. With a proboscis armature of 28-30 rows of 23-27 hooks *C. viarius* clusters with *C. albidus* and *C. polymorphus* each of which has up to 30 rows of hooks (Lunaschi & Drago, 2010).

In terms of number of hooks per row *C. viarius* is closest to *C. albidus*, but differs in the number and type of hooks per row (8-9+4-5+12-13 compared with 7-8+3-4+10). The hooks of *C. viarius*, are smaller and more variable in size, 18-40 for hooks with roots and 10-30 for spiniform hooks, compared with 44 for hooks on the first third of the proboscis and 35 elsewhere for *C. albidus* (Schmidt & Neiland, 1966). None of the specimens of *C. viarius* examined in this study had hooks with reduced roots and manubria as figured by Schmidt & Neiland (1966). *Centrorhynchus viarius* further differs from *C. albidus* in the number of cement glands (4, as determined by transverse section, for *C. viarius*, 3 for *C. albidus*) (Schmidt & Neiland, 1966). Both species occur in Falconidae from Paraguay but *C. viarius* has been found in hawks, *Buteo magnirostris*, *Buteogallus meridionalis*, *B. urubitinga* and *Parabuteo uncinctus* while *C. albidus* has been reported from the plumbeous kite *Ictinia plumbea* (Gmelin, 1788) (see Golvan, 1956).

Of the species of *Centrorhynchus* also found in Paraguay *C. viarius* with a proboscis armature of 28-30 longitudinal rows of hooks is closest to *C. pitangi*, also with 28-30 rows of hooks. *Centrorhynchus viarius* differs from *C. pitangi* in the number of hooks per row (23-27 compared with 18-20) the form of the true hooks (all without manubria compared to hooks 1-4 with manubria and large simple roots and hooks 7-8 with manubria and reduced roots) as well as the number of spiniform hooks

(7-8 compared to 12-13). *Centrorhynchus viarius* is a longer worm than *C. pitangi* and has shorter lemnisci, smaller testes and smaller eggs (Table 3). *Centrorhynchus viarius* can be differentiated from *C. guira*, a larger worm, in the number of hooks per row (23-27 compared with 18-19), the form of the manubria of the transitional hooks and the number of spiniform hooks (6 compared with 12-13). *Centrorhynchus viarius* can be differentiated from *C. opimus* by the number of rows of proboscis hooks (24 compared with 28-30) and the form of the true hooks (all without manubria compared to some with manubria). *Centrorhynchus viarius* further differs from *C. geranoeti* and *C. millerae* in the number of hooks per row (23-27 compared with 22-24 and 16-20 respectively) and the form of the true hooks (males and females having all true hooks with large simple hooks and transitional hooks compared with males having some true hooks with reduced hooks and no transitional hooks) and from *C. simplex* in the number of rows and hooks per row. Comparative measurements are given in Table 3. *Centrorhynchus viarius* differs from *C. simplex* in proboscis armature (28-30 longitudinal rows of 23-27 hooks compared with 22-24 longitudinal rows of 22-24 hooks).

Of the four species of *Centrorhynchus* known only from North America *C. spinosus*, with 30-32 longitudinal rows of 23-28 hooks, has a similar proboscis armature to that of *C. viarius*. *Centrorhynchus spinosus*, a much larger worm (females up to 60 mm long), can be differentiated from *C. viarius* by having 8-9 true hooks, no transitional hooks and 13-15 spiniform hooks in each row. The females of *C. spinosus* have two genital papillae.

KEY TO THE NEOTROPICAL SPECIES OF *CENTRORHYNCHUS*; based on Lunaschi & Drago (2010).

- 1a Proboscis armature of 22-24 longitudinal rows of 24 hooks per row;
14 true hooks + 10 spines *C. simplex* Meyer, 1932
- 1b Proboscis armature not as above 2
- 2a Proboscis armature with manubria on some true hooks 3
- 2b Proboscis armature without manubria on true hooks 6
- 3a Proboscis armature without transitional hooks . *C. tumidulus* (Rudolphi, 1819)
- 3b Proboscis armature with transitional hooks 4
- 4a Proboscis armature of 28-30 longitudinal rows of 18-20 hooks per row;
8-9+2+7-8 *C. pitangi* sp. n.
- 4b Proboscis armature of less than 28 longitudinal rows of hooks 5
- 5a Proboscis armature of 24-28 longitudinal rows of 27-28 hooks per row;
16-17+1+10-11 *C. giganteus* Travassos, 1921
- 5b Proboscis armature of 24 longitudinal rows of 12-13 hooks; 8-9 true +
transitional hooks + 3-4 spines *C. opimus* Travassos, 1921
- 6a Proboscis armature with transitional hooks in female only 7
- 6b Proboscis armature with transitional hooks in both male and female 8
- 7a Proboscis armature with 30-32 longitudinal rows of 16-20 hooks per
row; male 6-7+9-14, female 5-6+3-4+10 transitionals with lateral pro-
cesses *C. millerae* sp. n.
- 7b Proboscis armature with 30 longitudinal rows of 22-24 hooks per row;
male 11-12+9-10, female 8-10+3-4+9-10 transitionals without lateral
processes *C. geranoeti* sp. n.

- 8a Proboscis armature with transitional hooks with lateral processes 9
 8b Proboscis armature with transitional hooks without lateral processes 10
 9a Proboscis armature with 26-35 longitudinal rows of 22-27 hooks per row; 7-9+2+14-18 *C. kuntzi* Schmidt & Neiland, 1966
 9b Proboscis armature with 30-32 longitudinal rows of 18-19 hooks per row; 8-9+4+6 *C. guira* Lunaschi & Drago, 2010
 10a Proboscis armature of more than 30 longitudinal rows of hooks 11
 10b Proboscis armature of up to 30 longitudinal rows of hooks 12
 11a Proboscis armature of 32-35 longitudinal rows of 15-17 hooks per row; 8-9+3+4-5 *C. crotophagicola* Schmidt & Neiland, 1966
 11b Proboscis armature of 36-38 longitudinal rows of 17-18 rows of hooks; 9+3+5 *C. microcephalus* Bravo Hollis, 1947
 12a Proboscis armature of 28-30 longitudinal rows of 20-22 hooks; 8+4+10 *C. albidus* Meyer, 1932
 12b Proboscis armature of 28-30 longitudinal rows of 23-27 hooks; 8-9+4-5+12-13 *C. viarius* sp. n.

Family Plagiorhynchidae

Lueheia inscripta (Westrumb, 1821)

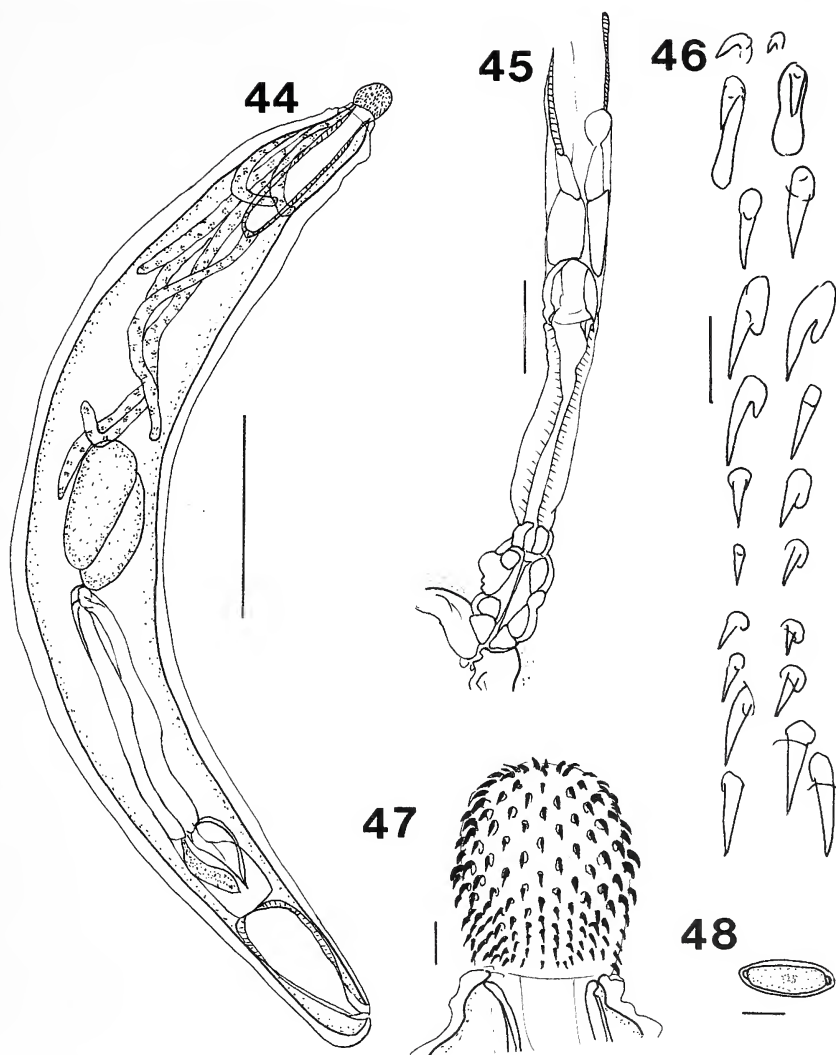
Figs 44 - 48

MATERIAL EXAMINED: MHNG-INVE-38401, MNHG-INVE-38402; voucher specimens, 2 males, 5 females, 20 juveniles, from small intestine, *Turdus amaurochalinus* Cabanis, 1850; Paraguay, S. Lorenzo N 10 E, 16.10.1987, 16.10.1989. – MHNG-INVE-48453; voucher specimen, 1 male, from small intestine, *T. amaurochalinus*; Paraguay, Pedro P Pena, 8.10.1986. – MHNG-INVE-38389; voucher specimens, 2 females, from small intestine, *Ardea alba* Linnaeus, 1758; Paraguay, Transchaco 180, 28.10.1988. – MHNG-INVE-38436; voucher specimens, 3 juveniles, from small intestine *Taraba major* (Vieillot, 1816); Paraguay, Transchaco 293, 04.07.1985. – MHNG-INVE-38400; 15 immature specimens, proboscides inverted, from small intestine, *T. major*; Paraguay, S. Lorenzo 10 E, 16.10.1989. – MHNG-INVE-38399. 1 female, *Synallaxis* sp. S. Lorenzo N 10 E, 16.10.1989.

REDESCRIPTION

General: [Based on 3 males, 4 females, 40 immature or juvenile specimens and Travassos (1926)]. Trunk spineless, elongated, fusiform. Proboscis subglobular to semispherical; armed with 28-30 rows 9-12 hooks; largest hooks located mid proboscis, first and last 2 hooks in row 17-25 long, other hooks 40-56 long. Neck spineless, short, longer than wide in female. Proboscis receptacle double walled. Lemnisci 2, each subdivided into 3 long slender parts of varying lengths inserted at base of neck, extend posteriorly reaching beyond anterior testis. Cerebral ganglion located at mid region of proboscis receptacle.

Male: Trunk 8-11 (9.5) mm long, 1200-1530 (1365) wide. Proboscis 380-600 (480) long, 310-430 (400) wide. Neck 348 long, 348 wide at base. Proboscis receptacle 1375-1615 (1530) long, 320-340 (330) wide; lemnisci (single measurement) longest parts 4760, shortest parts 2550. Testes oval, contiguous, in middle third of trunk; anterior testis 1000-1205 (1135) long, 400-630 (522) wide; posterior testis 1000-1200 (1075) long, 375-500 (460) wide. Cement glands, 4, (by dissection) elongated, tubular, begin immediately posterior to end of posterior testis, 1900-2550 (2385) long. Genital pore subterminal. Entire male system occupies about 65% of trunk length.



FIGS 44-48

Lueheia inscripta (Westrumb, 1821) (44) Male. (45) Female reproductive tract. (46) Proboscis hooks, longitudinal rows of 11 hooks. (47) Female proboscis, showing armature. (48) Egg. Scale bars: 44, 1 mm; 45, 150 μ m; 46, 48, 25 μ m; 47, 100 μ m.

Female: Trunk 7-15 (10.4) mm long, 1870-2200 (1990) wide. Proboscis 425-530 (477) long, 402-420 (410) wide just anterior to constriction. Hook lengths 2 longitudinal rows 25, 23; 42, 40; 50, 49; 49, 50; 45, 49; 45, 40; 40, 40; 40, 40; 50, 40; 35, 25; 30, 25. Neck 201 long, 445 wide at base. Proboscis receptacle 1570-1700 (1637) long, 300-325 (312) wide. Reproductive tract, uterine bell to genital pore, 1070-1140 (1105). Genital pore subterminal. Eggs oval, external shell thick, with polar protrusions of the fertilization membrane, 59.5-78.0 (63.0) long, 23.0-28.0 (24.0) wide.

COMMENTS: Although identified as early as 1821 (Westrumb) and redescribed by Travassos (1926) from specimens occurring in Turdidae from Brazil, the descriptions of *L. inscripta* were brief and gave only limited morphometric data, especially for females. More recently Whittaker *et al.* (1970b) reported *L. inscripta* from grackles, *Quiscalis niger* (Boddaert, 1783) and Acholonu (1976) reported juvenile males and females from lizards *Anolis cristatellus* Duméril & Bibron, 1837 from Puerto Rico. Subsequently Salgado-Maldonado & Caspeta-Mandujano (2010) reported on juveniles in frogs, *Lepidodactylus fragilis* Brochi, 1877 and a toad *Bufo marinus* (Linnaeus, 1758). These latter authors provided comprehensive descriptions of both male and female juveniles and demonstrated that the morphology and morphometrics of their specimens from paratenic hosts were congruent with those of adult specimens of *L. inscripta* from passerine birds (Table 4).

Although *L. inscripta* and *L. adlueheia* have been considered synonyms by some authors (see for example Schmidt & Neiland, 1966), they should now both be accepted as valid species, on the basis of reexamination of specimens and reevaluation of characters (Van Cleave & Williams, 1952; Salgado-Maldonado & Caspeta-Mandujano, 2010). Both *L. inscripta* and *L. adlueheia* have similar proboscis armature (28-30 longitudinal rows of 9-12 hooks compared with 28 rows of 9-10 hooks) and hook size (largest blades 63 compared with 62 long) but they can be distinguished by a suite of other characters. *Lueheia inscripta* differs from *L. adlueheia* in having a larger proboscis, shorter cement glands, longer Saeftigen's pouch, larger eggs and the number of branches of the lemnisci and their lengths (4-6 of varying lengths compared with 6-10 of similar lengths) (Table 4).

Lueheia inscripta differs from the type species *L. lueheia* in proboscis armature (28-30 rows of 9-12 hooks compared with 20-22 rows of 8-9 hooks). Both species have 6 lemnisci but those of *L. inscripta* are of varying lengths while those of *L. lueheia* are of similar lengths. The testes of *L. inscripta* are larger (1000-1205 long compared with 700) and the eggs smaller (59.5-78 by 23-28 compared with 78-80 by 28-31) (Travassos 1921, 1926).

The proboscis armature of *L. cajabambensis* is not described except to say that the form and number of hooks differs from those of *L. lueheia* and *L. inscripta*. *Lueheia inscripta* further differs from *L. cajabambensis* in having up to 6 lemnisci compared with only 4, smaller testes (1000-1205 compared with 1748-1992 long), shorter cement glands (1900-2550 compared with 4834) and shorter Saeftigen's pouch (600-700 compared with 1909) (Machado-Filho & Nicanor-Ibáñez, 1967).

A new species, *L. karachiensis*, was described from 3 males occurring in *A. b. cenchroides* from Karachi, Pakistan. As described, the only character suggesting that these specimens are of the genus *Lueheia* is the presence of 4 lemnisci. The body shape of this species both from the description and figure appears more like *Centrorhynchus* than *Lueheia* as does the placement of testes in anterior third of the trunk and the proportions of the reproductive system. The description of the proboscis, subglobular with no measurements given, differs from the more or less cylindrical shape depicted in the figure. The roots of the proboscis hooks are neither described nor drawn (Aly Khan *et al.*, 2005). Given that the other four species of *Lueheia* are found in passerine birds from the Americas and this species in a raptor from the Indian subcontinent it seems most

TABLE 4. Comparative information for *Lueheia inscripta* (Wertheim, 1821) and *L. adlueheia* (Werby, 1938). *This measurement may be in error.

	<i>L. inscripta</i>	<i>L. inscripta</i> juveniles	<i>L. inscripta</i>	<i>L. adlueheia</i>
Reference	Travassos, 1926	Salgado-Maldonado & Caspeta- Mandujano, 1910	this study	Werby, 1938
Male				
Trunk length mm	8	2.4-3.6	8-11	3.5-9.2
Proboscis length	520-620	420-560	380-600	385-490
width	410-430	330-380	310-430	280-385
Neck length		190-270	348	126-210
width		270-330	348	
Proboscis receptacle length	1600	732-1108	1375-1615	749-1190
width	340	297-346	320-340	
Lemnisci, number	4-6	6	6	6-10
length		891-1336	2250-4760	840-1820
Anterior testis length	1000	270-366	1000-1205	231-1274
width	400-500	75-200	400-630	120-177
Posterior testis length		237-375	1000-1200	280-1267
width		62-265	375-500	154-776
Cement glands	1900	740-1087	1900-2550	700-3430
Saefftiigen's pouch		28-43*	600-700	200-400
Female				
Trunk length mm	9-15	4.0-4.7	7-15	11.3-15
Proboscis length		540-610	425-530	399-602
width		370-410	402-420	315-525
Reproductive tract length	1900	800-1100	1070-1140	
Egg length	63-78		59.5-78	36-41
width	28		23-28	12.7-15.5
Hosts	Turdidae	Anura	Turdidae	Turdidae
Locality	Brazil	Mexico	Paraguay	Washington USA

likely that *L. karachiensis* should be re assigned, possibly to the genus *Centrorhynchus*. Multiple lemnisci have been recorded as anomalies in *Fillicollis sphaerocephalis* (Bremser in Rudolphi, 1819) now *Profillicollis sphaerocephalis*, *Pomphorhynchus proteus* now a synonym of *P. laevis* (Mueller, 1776) and *Plagiorhynchus formosus* now a synonym of *P. cylindraceus* (Goeze, 1782) (see Van Cleave, 1942) and could perhaps be the case in this instance. Until the identity of this species is resolved it should be relegated to incertae sedis.

DISCUSSION

Consistent characters for recognizing and defining acanthocephalans include the dimensions and morphology of the proboscis and its armature (Richardson & Nickol, 1995). For species of *Centrorhynchus* in particular, the number of longitudinal rows of hooks, number of hooks per row, size of blades and morphology and size of roots have great taxonomic value (Golvan, 1960). The morphology of the hooks: true (simple roots with or without manubria), transitional (reduced roots with manubria, with or without lateral alate processes) and spiniform (reduced roots without manubria), is consistently reliable and was used by Lunaschi & Drago (2010) in their key to Neotropical species of *Centrorhynchus*. An analysis of hook morphology suggests that the South American fauna can be grouped into species having some true hooks with manubria, *C. giganteus*, *C. opimus*, *C. pitangi*, and *C. tumidulus* and species having all

true hooks without manubria, *C. albidus*, *C. crotophagicola*, *C. geranoaeti*, *C. guira*, *C. kuntzi*, *C. microcephalus*, *C. millerae*, *C. nicaraguensis*, *C. pitangi*, *C. polymorphus*, *C. viarius*. Alternatively all, with the exception of *C. tumidulus*, found in Brazil, Columbia, Uruguay and Venezuela in South America and Panama in Central America, fall into a single group with transitional hooks. Additional evidence is needed however before potential relationships between these species can be determined.

The species occurring in Paraguay fall into two groups, those with lateral alate processes on the transitional hooks (*C. geranoaeti*, *C. guira*, and *C. millerae*) and those without (*C. albidus*, *C. pitangi* and *C. viarius*). Within the former group *C. geranoaeti* and *C. millerae* share the character of sexual dimorphism of the proboscis armature as well as that of the form of the transitional hooks suggesting a possible relationship between them and *C. guira* and *C. kuntzi* the only other species with lateral alate processes. *Centrorhynchus guira* is found in Argentina and Paraguay, *C. kuntzi* in The Galapagos, Nicaragua, Central America and Florida, United States of America. Each of the species in the latter group has a proboscis armature of 28-30 longitudinal rows of hooks. *Centrorhynchus pitangi* can also be linked with *C. giganteus*, *C. opimus* and *C. tumidulus* in having some true hooks with manubria. *Centrorhynchus giganteus* and *C. tumidulus* are also known from Panama, Central America and *C. opimus* only from Brazil. *Centrorhynchus albidus* and *C. viarius* share the characters of number of longitudinal rows of hooks and true hooks without manubria.

Centrorhynchus opimus Travassos, 1921 was originally described from the great kiskadee, *Pitangus sulfuratus* (Passeriformes: Tyrannidae), from Brazil and subsequently transferred to *Sphaerirostris* by Golvan (1956, 1960) because of the morphology of the hooks and its occurrence in passerine bird hosts. It has since been reported from Brazil, as *C. opimus* from the boat billed flycatcher, *Megarhynchus pitangua* (Linnaeus, 1766) (Vicente *et al.*, 1983) and was returned to *Centrorhynchus*, without discussion, by Golvan (1994). Lunaschi & Drago (2010) however did not include *C. opimus* in their key. A comparison of the generic diagnoses of *Centrorhynchus*, parasites of diurnal and nocturnal birds of prey and *Sphaerirostris*, parasites of the passerine families Turdidae, Corvidae and related families, to the descriptions of *C. opimus* by Travassos (1921, 1926) suggests that the cylindrical shape of the body and the elongated shape of the proboscis, as figured by Travassos (figs 25, 26, plate 10 and 27, plate 11, 1926) and Vicente *et al.* (fig. 10, 1983), are typical of *Centrorhynchus* spp. and not *Sphaerirostris* spp. Richardson & Nickol (1995) emphasized the importance of trunk shape as a useful characteristic. Golvan (1960) suggested that true hooks with manubria, as described for *C. opimus*, were seen only in the proboscis armature of species of *Sphaerirostris* but both *C. giganteus* occurring in Falconidae from Brazil and *C. pitangi* (this study) have true hooks with manubria (Travassos, 1926; Lunaschi & Drago, 2010). Hence true hooks, with and without manubria, are found in both genera. Moreover a species of *Centrorhynchus*, from Mexico *C. microcephalus* has been described from the passerine family Icteridae (see Richardson & Nickol, 1995), broadening the host range of some species of *Centrorhynchus* to selected passerine families. Therefore, since the shape and size of the body and proboscis of *C. opimus* better fits *Centrorhynchus* than *Sphaerirostris* and similarly shaped hooks are found in both genera, the placement of *C. opimus* is justified.

The taxonomic position of *C. polymorphus* has been previously suggested as equivocal (Dimitrova & Gibson, 1995; Lunaschi & Drago, 2010). Given the shape and size of the body and the proboscis these authors were of the opinion that *C. polymorphus* better fit *Sphaeroirostris* than *Centrorhynchus*. This is the same logic as was applied to the placement of *C. opimus* and is supported here. Therefore the Centrorhynchidae now known to occur in South America include 13 species of *Centrorhynchus*: *C. albidus*, *C. crotophagicola*, *C. geranoaeti*, *C. giganteus*, *C. guira*, *C. kuntzi*, *C. microcephalus*, *C. millerae*, *C. nicaraguensis*, *C. opimus*, *C. pitangi*, *C. tumidulus*, *C. viarius* as well as one species yet to be fully described and a species of *Sphaeroirostris*; *S. polymorphus*.

ACKNOWLEDGEMENTS

My thanks go to Prof. Mariaux for access to the specimens, assistance with collection data and hospitality in Geneva. Librarians from Central Queensland University provided interlibrary loan services.

REFERENCES

- ACHOLONU, A. D. 1976. Helminth fauna of saurians from Puerto Rico with observations on the life cycle of *Lueheia inscripta* (Westrumb, 1821) and description of *Allopharynx peurtoricensis* sp. n. *Proceedings of the Helminthological Society of Washington* 43: 106-116.
- ALY KHAN, BILQUEES F. M. & MUTI-UR-REHMAN 2005. *Lueheia karachiensis*, new species (Acanthocephala: Plagiorhynchidae) from a bird in Karachi, Pakistan. *Pakistan Journal of Zoology* 37: 113-115.
- AMIN, M. O. 1985. Chapt 4. Classification. In: CROMPTON, D. W. T. & NICKOL, B. B. (eds). *Biology of the Acanthocephala*. Cambridge University Press, Cambridge, 519 pp.
- CALEGARO-MARQUES, C. & AMATO, S. B. 2010. Parasites as secret files of the trophic interactions of hosts: the case of the rufous-bellied thrush. *Revista Mexicana de Biodiversidad* 81: 801-811.
- DIMITROVA, Z. M. & GIBSON, D. I. 2005. Some species of *Centrorhynchus* Lühe, 1911 (Acanthocephala: Centrorhynchidae) from the collection of the Natural History Museum, London. *Systematic Parasitology* 62: 117-134.
- GOLVAN, Y. 1956. Le genre *Centrorhynchus* Lühe 1911 (Acanthocephala-Polymorphidae) Révision des espèces européennes et description d'une nouvelle espèce africaine parasite de rapace diurne. *Bulletin de l'Institut Français d'Afrique Noire* 20: sér. A: 732-785.
- GOLVAN, Y. J. 1960. Le Phylum Acanthocephala 3^e note La classe des Paleacanthocephala (Meyer, 1931). *Annales de Parasitologie* 35: 575-593.
- GOLVAN, Y. J. 1994. Nomenclature of the Acanthocephala. *Research and Reviews for Parasitology* 54: 135-205.
- LUNASCHI, L. I. & DRAGO, F. B. 2010. A new species of *Centrorhynchus* (Acanthocephala, Centrorhynchidae) endoparasite of *Guira guira* (Aves, Cuculidae) from Argentina. *Helminthologia* 47: 38-47.
- MACHADO-FILHO, D. A. & NICANOR-IBÁÑEZ, H. 1967. Fauna Helminthologia do Peru: *Lueheia cajabambensis* sp.n. (Acanthocephala, Echinorhynchidae). Nota previa *Atas da Sociedade de Biologia do Rio de Janeiro* 10: 157-158.
- PETROCHENKO, V. I. 1958. Acanthocephala of Domestic and Wild Animals Vol. II. *Izdatel'stva Akademii Nauk SSSR, Moskva*. Translated from the Russian, Israel Program for Scientific Translations Jerusalem, 1971. 478 pp.
- RICHARDSON, D. J. & NICKOL, B. B. 1995. The genus *Centrorhynchus* (Acanthocephala) in North America with descriptions of *Centrorhynchus robustus* n. sp., and redescription of *Centrorhynchus conspectus*, and a key to the species. *Journal of Parasitology* 81: 767-772.

- SALGADO-MALDONADO, G. & CASPETA-MANDUJANO, J. M. 2010. *Lueheia inscripta* (Westrumb, 1821) (Acanthocephala: Plagiorhynchidae) in Anurans (Leptodactylidae: Bufonidae) from Mexico. *Parasite* 17: 161-165.
- SCHMIDT, G. D. & KUNTZ, R. E. 1967. Revision of the Porrorchinae (Acanthocephala: Plagiorhynchidae) with descriptions of two new genera and three new species. *Journal of Parasitology* 53: 130-141.
- SCHMIDT, G. D. & NEILAND, K. A. 1966. Helminth fauna of Nicaragua III. Some Acanthocephala of birds including three new species of *Centrorhynchus*. *Journal of Parasitology* 52: 739-745.
- TANTALEÁN, M., SÁNCHEZ, L., GÓMEZ, L. & HIZA, A. 2005. Acantocéfalos del Perú. *Revista Peruana de Biología* 12: 83-92.
- TRAVASSOS, L. 1921. Contribuição para o conhecimento dos acantocéfalos da sub-família Centrorhynchinae. *Folia Medica* 2: 42-43.
- TRAVASSOS, L. 1926. Contribuições para o conhecimento da fauna helminthological brasileira. 20. Revisão dos acanthocephalos brasileiros Parte II Família Echinorhynchidae Hamann, 1892, sub-fam. Centrorhynchinae Travassos, 1919. *Memórias do Instituto Oswaldo Cruz*. 19: 31-125.
- VAN CLEAVE, H. J. 1942. A reconsideration of *Plagiorhynchus formosus* and observations on Acanthocephala with atypical lemnisci. *Transactions of the American Microscopical Society* 61: 206-210.
- VAN CLEAVE, H. J. & WILLIAMS, R. B. 1951. Acanthocephala from passerine birds in Alaska. *The Journal of Parasitology* 37: 151-159.
- VICENTE, J. J., PINTO, R. M. & NORONHA, D. 1983. *Skryabinoclava tupacincal* Freitas, Vicente & Ibanez, 1970 in Brazil and some other helminths from Tyrannidae birds. *Memórias do Instituto Oswaldo Cruz* 78: 95-100.
- VIZCAINO, S. I. 1993. Presencia del genero *Centrorhynchus* Luhe, 1911, (Acanthocephala: Centrorhynchidae) en la Republica Argentina. *Neotropica (La Plata)* 39: 101-102.
- WERBY, H. T. 1938. A new genus of Acanthocephala with forked lemnisci. *Transactions of the American Microscopical Society* 57: 204-212.
- WHITTAKER, F. H., SCHMIDT, G. D. & GARCIA DIAZ, J. 1970a. Helminth parasites of the cattle egret in Puerto Rico. *Proceedings of the Helminthological Society of Washington* 37: 262.
- WHITTAKER, F. H., SCHMIDT, G. D. & GARCIA DIAZ, J. 1970b. Helminth parasites of some birds in Puerto Rico. *Proceedings of the Helminthological Society of Washington* 37: 123-124.
- YAMAGUTI, S. 1963. Acanthocephala. *Systema Helminthum* Vol. V Interscience, New York, 423 pp.

**An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève,
Part 4: The Acridomorpha excluding the superfamily Acridoidea**

John HOLLIER

Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Switzerland.

Email: John.Hollier@ville-ge.ch.

An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève, Part 4: The Acridomorpha excluding the superfamily Acridoidea. - Henri de Saussure described 58 species or subspecies in the infra-order Acridoidea (excluding the superfamily Acridoidea, which is treated elsewhere). The taxon names are listed alphabetically, and the location of the type material (if known) and the current nomenclatural combination are given. When there is primary type material in the Muséum d'histoire naturelle de Genève (MHNG) the sex, label data and condition of the specimens is given, along with their location within the collection.

Keywords: Caelifera - Tetrigoidea - Eumastacoidea - Pyrgomorphidea - Trigonopterygoidea - type-catalogue.

INTRODUCTION

Henri de Saussure (1829-1905) was a prolific taxonomist probably best known for his work on the orthopteroid insects. Details of his career can be found in the introduction to the first part of the catalogue (Hollier & Heads, 2012). The species described by Saussure in the Acridomorpha are listed by Hollier (2012a, 2012b). Saussure made great use of the collection of Brunner von Wattenwyl (1823-1914), most of which is now in the Naturhistorisches Museum (NHMW) in Vienna. Other material studied by Saussure is in the Natural History Museum (BMNH) in London and the Muséum National d'Histoire Naturelle (MNHN) in Paris.

Type material of 37 species has been identified in the collection of the Geneva Natural History Museum (MHNG). Material which was in other collections at the time of publication has been located where possible but there are 7 species unaccounted for. It is possible that some type material is to be found amongst the series placed under the name of what Saussure assumed (whether correctly or not) was the senior synonym or amongst the duplicate and depot material having lost any labels that identify it as such (Carbonell in lit.).

ARRANGEMENT AND FORMAT

The species are listed alphabetically. The format for each is:

species name Author, work: page [*Original generic placement*].

Type locality as given in the original description and depository. Type series. Number of specimens. Specimen: "Label data" [format of label]. Following the recommendations of Ohl & Oswald (2004) the condition of each specimen is noted. Other comments. Location of material in the MHNG main Orthoptera collection. Currently valid binomen of taxon (following Eades *et al.*, 2012).

The following additional abbreviations are used in the list.

BMNH The Natural History Museum, London

HNHM Hungarian Natural History Museum, Budapest

MHNG Muséum d'histoire naturelle, Geneva

MNHN Muséum National d'Histoire Naturelle, Paris

MNMS Museo Nacional de Ciencias Naturales, Madrid

NHMW Naturhistorisches Museum Wien, Vienna

OSF Orthoptera Species File Online (Eades *et al.*, 2012)

OXUM Oxford University Museum of Natural History, Oxford

SMFD Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt

CATALOGUE

acutipennis Saussure, 1903b: 78-79, fig. 8 [*Erianthus*].

Khavi (Regiones indicae) (Mus. Genavense). One ♀.

Holotype ♀ with labels: "Khasi H" [printed on white card]; "*Erianthus acutipennis* Sauss., ♀, Khasi" [handwritten on yellow paper]; "*Khaverianthus acutipennis* (Sauss.) n. gen., M. Descamps det. 1974" [handwritten on white card with "M. Descamps det. 19" printed]; "Holotypus" [printed on red card]. Specimen set with right wings spread and left wings folded: the right antenna, the tarsi of the left middle leg and both hind legs are missing. Box S1.

Khaverianthus acutipennis (Saussure, 1903).

alligator Saussure, 1861b: 483-484 [*Scelymena*].

L'île de Ceylan, Kaduganawa (leg. Humbert). Unspecified number of ♂.

No specimens found in the MHNG collection. The ♂ described was almost certainly a juvenile of *S. crocodilum* Saussure, 1861 but could not be identified amongst the specimens placed under that name in the collection.

A junior synonym of *Gavialidium crocodilum* (Saussure, 1861).

azteca Saussure, 1861a: 400 [*Tettix*].

Mexico calida. Unspecified.

Lectotype ♀ (designated by Rehn & Grant, 1957: 294) with labels: "Potrero, Sumichrast" [handwritten on white paper]; "*Paratettix aztecus* Sauss." [handwritten in green paper]; "Musée de Genève, *Paratettix azteca* S." [determination handwritten on printed white card]; "TYPE selected by Rehn and Grant 1956, *Tettix azteca* Sauss."

[handwritten on red card with "TYPE" printed]. Specimen set with wings folded; both antennae and the last tarsal segment of the left hind leg are missing. There are also six paralectotypes. Box Q5.

Paratettix aztecus (Saussure, 1861).

aztecus Saussure in Bolívar, 1884: 442-443 [*Xyronotus*].

Méjico (coll. Scudder, Saussure, Bolívar). Unspecified number of ♂ and ♀.

The lectotype ♂ (designated by Kevan, 1952: 269) is in the OXUM. The MHNG collection contains seven ♂ and nine ♀ paralectotypes and some nymphs which might also have been syntypes. Dirsh & Mason (1979: 202) refer to the lectotype without stating where it is. They also consider that both genus and species should be considered Bolívar's, although this has not been generally accepted. Images on OSF. Box X6.

Xyronotus aztecus Saussure, 1884.

birmanicus Saussure, 1903b: 82, fig.12 [*Erianthus*].

Birmania, Bhamo (Mus. Genavense). One ♂.

Holotype ♂ with labels: "Bhamò, Birmanie, Fea IX 1885" [printed on white card with "IX" and "5" handwritten]; "Erianthus Birmanicus Sauss., Bhamo" [handwritten on yellow paper]; "Erianthina deflorata (Brunner 1893) n. gen., M. Descamps det. 1974" [handwritten on white card with "M. Descamps det. 19" printed]; "Holotypus" [printed on red card]. Specimen set with right wings spread and left wings folded; most of both antennae, the right middle leg, the last tarsal segment of the left hind leg and the tarsi of the right hind leg are lost. Box S1.

A junior synonym of *Erianthina versicolor* (Brunner von Wattenwyl, 1893).

bispina Saussure, 1861a: 401 [*Tettix*].

Brasilia, Bahia. Unspecified.

The MHNG collection contains a single ♂ specimen under this name, but this is labelled "PEROU CENT. 115" and "bispina? Sauss, Perou" and so is not part of the type series. The whereabouts of the type material is unknown. Box Q1.

Cota bispina (Saussure, 1861).

brevipennis Saussure, 1899: 647 [*Maura*].

Africa meridionalis. More than one ♀.

Two ♀ syntypes. A ♀ with labels: "Delagoa, 5427/4" [printed on rhomboid of white card]; "Maura brevipennis Sauss." [handwritten on pink paper]; "LECTOTYPE, (SYNTYPE), Det. D.K.McE. Kevan, 1960" [handwritten on white card with "Det. D.K.McE. Kevan, 195" printed]. Specimen set with wings folded; the right front and middle legs are lost. A ♀ with labels: "Delagoa Bay, Junod" [handwritten on white paper]; "Maura brevipennis Sauss." [handwritten on pink paper]; "SYNTYPE, Det. D.K.McE. Kevan, 1960" [handwritten on white card with "Det. D.K.McE. Kevan, 195" printed]. Specimens set with wings spread; the abdomen is rather shrivelled. The lectotype does not seem to have been formally designated. Box X15.

A junior synonym of *Maura rubroornata* (Stål, 1855).

brevipennis Saussure, 1903b: 93-94, fig. 14 [*Paramastax*].

Peruvia centralis (Mus. Genavense). Two ♂.

Lectotype ♂ (designated by Descamps, 1970: 623) with labels: "PEROU CENT, 103" [locality printed and numerals handwritten on white paper]; "Paramastax brevipennis Sauss., Perou centr." [handwritten on green paper]; "Paramastax brevipennis Sss., Hololectotypus [sic]; C S Carbonell. 1966" [handwritten by Carbonell on red card]; "Lectotype designated Descamps 1970" [handwritten on red paper]. Specimen set with right wings roughly spread and left wings roughly folded; most of both antennae and both hind legs are lost. A micro-tube with dissected parts is secured on a separate pin. There is also a ♂ paralectotype. Images on OSF. Box S2.

Pseudomastax brevipennis (Saussure, 1903).

caiman Saussure, 1861a: 402 [*Amorphopus*].

Brasilia. Unspecified.

One ♂, possibly a syntype, with labels: "Brésil, Mr Hy de Sauss." [locality handwritten on printed white paper]; "33. Amorphopus notabilis, Bolivar det." [handwritten on white paper]; "Possible syntype of *A. caiman* Sauss., Hollier 2011" [handwritten on red paper]. Specimen set with wings folded; the left antenna, two tarsal segments of the right front leg, right middle leg and left middle leg, the tibia and tarsi of the left hind leg and the tarsi of the right hind leg are lost. This specimen was placed under *A. notabilis* Serville in the MHNG collection but the measurements coincide with those of the rather rudimentary original description. Box Q4.

A junior synonym of *Amorphopus notabilis* Serville, 1838.

caudata Saussure, 1861a: 399-400 [*Tettix*].

Guyana. Unspecified number of ♂ and ♀.

One ♂ syntype with labels: "Guy." [printed on white card]; "103" [handwritten on green paper]; "Syntypus" [printed on red paper]. Specimen set with wings folded; the right antenna, right middle leg and right hind leg are lost. Two ♀ specimens labelled "CAYENNE" may also be syntypes. Box Q6.

Micronotus caudatus (Saussure, 1861).

chichimeca Saussure, 1861a: 400-401 [*Tettix*].

Mexico calida. Unspecified.

No specimens found in the MHNG collection. The whereabouts of the type material is unknown.

Tettigidea chichimeca (Saussure, 1861).

congensis Saussure in Riley, 1893: 581 [*Atractomorpha*].

Congo. Eleven specimens (both sexes represented).

No specimens found in the MHNG. No description was given in the original publication and so *A. congensis* is a *nomen nudum*. Kevan (1960: 40) found the material seen by Saussure in the Smithsonian Museum and nominated a ♂ "pseudotype", identifying it as *A. gerstaeckeri* Bolivar.

A junior synonym of *Atractomorpha acutipennis gerstaeckeri* Bolivar, 1884.

coniceps Saussure, 1903a: 414-415 [*Malagassa*].

Madagascar (Mus. Genavense, leg. Sikora). Unspecified number of ♂ and ♀.

Lectotype ♂ (designated by Descamps, 1965: 49) with labels: "Malagassa coniceps Sauss., ♂, Madagaskar" [handwritten on pink paper]; "Musée Senkenberg[sic]" [printed on white paper]; "LECTOTYPE" [printed on red card]. Specimen lacks both antennae, the last tarsal segment of the left front leg, the right front leg, the left middle leg and the last tarsal segment of the right hind leg. Box S2.

Malagassa coniceps Saussure, 1903.

consobrina Saussure, 1861b: 475 [*Atractomorpha*].

Ile de Ceylan. Unspecified.

Lectotype ♂ (designated by Kevan, 1963: 80) with labels: "♂" [printed on white card]; "205" [handwritten on white paper]; "Trincomalie, Ceylan, V^{ge} Humbert" [handwritten on white paper]; "LECTOTYPE of *Atractomorpha consobrina* Sss, Det. D.K.McE. Kevan, 1960, = *crenulata* F." [handwritten by Kevan on white card with "Det. D.K.McE. Kevan, 19" printed]. There is also a ♀ paralectotype. Box X3.

A junior synonym of *Atractomorpha crenulata crenulata* (Fabricius, 1793).

cordillierae Saussure, 1903a: 413-414 [*Scirtomastax*].

Equateur, Ambatao (coll. Finot). One ♀.

No specimens found in the MHNG collection. The ♀ holotype was in the collection of Finot when the description was published, and is now in the MNHN (images on OSF).

Paramastax cordillierae (Saussure, 1903).

crassipes Saussure, 1903a: 414 [*Xanthomastax*].

Celebes septentrionalis, Toli-Toli (Mus. Genavensis). Unspecified number of ♂.

One ♂ syntype with labels: "Nord-Celebes, Toli Toli, Nov.-Dez. 1895, H. Fruhstorfer" [printed on white card]; "*Xanthomastax crassipes* Sauss., Nord-Celebes" [handwritten on yellow paper]; "Holotypus" [printed on red card]; "Type series unspecified: treat as syntype. Hollier 2011" [handwritten on red paper]. Specimen originally set with wings spread, but the left wings are missing; both antennae, the last tarsal segment of the right middle leg and the last tarsal segment of the left hind leg are missing. Willemse (1931: 206) recognised that *X. crassipes* was a junior homonym of *Mnesicles crassipes* Karsch, 1889 and proposed the replacement name *Mnesicles saussurei*. However, this in turn is a junior homonym of *Mnesicles saussurei* Bolivar, 1914, and the oldest valid available synonym has been applied. Box S2.

Mnesicles saobensis (Descamps, 1974).

crocodilum Saussure, 1861b: 481-483 [*Scelymena*].

Ile de Ceylan, Kaduganawa, 1000ft. (leg. Humbert). Numerous ♂ and ♀ captured *in copula*.

Six ♂ and three ♀ syntypes. A ♂ with labels: "CEYLON HUMB" [printed on a strip of white paper]; "*Gavialidium crocodilus* Sauss." [handwritten on yellow paper]; "14. *Gavialidium crocodilus*, Boliv. del." [handwritten on white paper];

"Syntypus" [printed on red paper]. Specimen set with wings folded; the right middle and hind legs are lost. A ♂ with labels: "CEYLON HUMB" [printed on a strip of white paper]; "Gavialidium crocodilus Sauss." [handwritten on yellow paper]; "Syntypus" [printed on red paper]. Specimen set with wings folded; the antennae are missing. A ♂ with labels: "286" [handwritten on bluish paper]; "CEYLON HUMB" [printed on a strip of white paper]; "Gavialidium crocodilus Sauss." [handwritten on yellow paper]; "Sc. crocodilum Sauss., Ceylan, M. Humbert" [handwritten on white paper]; "Syntypus" [printed on red paper]. Specimen set with hind wings roughly spread; the left antenna, the tibia and tarsi of the left middle leg, the tarsi of the right middle leg and the right hind leg are lost. A ♂ with labels: "Kadunganawa, Ceylon, V^{ge} Humbert" [handwritten on white paper]; "Gavialidium crocodilus Sauss." [handwritten on yellow paper]; "Syntypus" [printed on red paper]. Specimen set with wings folded; the left antenna, the right front leg, the tarsi of the left middle leg and both of the hind legs are missing. A ♂ mounted above a ♀ on one pin with labels: "286" [handwritten on bluish paper]; "CEYLON HUMB" [printed on a strip of white paper]; "Gavialidium crocodilus Sauss." [handwritten on yellow paper]; "Syntypus" [printed on red paper]. The ♂ set with wings folded; the antennae, the claw of the left front leg and the right middle leg are missing. The right hind leg is detached and glued to a card secured on the original pin. The ♀ set with wings folded; the right antenna, the tibia and tarsi of the right middle leg and the right hind leg are lost. A ♂ mounted above a ♀ on one pin with labels: "286" [handwritten on bluish paper]; "Gavialidium crocodilus Sauss." [handwritten on yellow paper]; "Syntypus" [printed on red paper]. The ♂ set with wings folded; the antennae, the tibia and tarsi of the right middle leg and both of the hind legs are lost. The ♀ set with wings folded; both antennae, the tibia and tarsi of the left hind leg and the right hind leg are lost. The femur of the left hind leg appears to have been reattached with glue. A ♀ with labels: "286" [handwritten on bluish paper]; "CEYLON HUMB" [printed on a strip of white paper]; "Gavialidium crocodilus Sauss." [handwritten on yellow paper]; "Syntypus" [printed on red paper]. Specimen set with wings folded; the left antenna is missing. Box Q2.

Gavialidium crocodilum (Saussure, 1861).

dentatus Saussure, 1903b: 91 [*Eumastax*].

Costa-Rica, Palmares (coll. Finot). One ♀.

No specimens found in the MHNG collection. The ♀ holotype was in the collection of Finot when the description was published and is now in the MNHN.

Homeomastax dentata (Saussure, 1903).

elegans brevipennis Saussure, 1899: 643 [*Zonocerus*].

Africa meridionalis, Gallaland. Unspecified.

Lectotype ♀ (designated by Kevan, 1977: 220) with labels: "Gallaland" [handwritten on pink card]; "Zonocerus elegans Thunb." [handwritten on pink paper]; "LECTO-TYPE" [printed on white card disk with purple border]; "LECTOTYPE selected, Det. D.K.McE. Kevan, 1971, SYNTYPE of Zonocerus elegans var. brevipennis, Saussure 1899. Det. D.K.McE. Kevan, 1971" [handwritten on white card with "Det. D.K.McE. Kevan, 19" printed twice]. Specimen lacks two tarsal segments of the

left front leg and the left hind leg. There is also a ♀ paralectotype with the same data. Box X9.

A junior synonym of *Zonocerus elegans elegans* (Thunberg, 1815).

facialis Saussure, 1903b: 97 [*Paramastax*].

Sarayacu (Mus. Genavense). Unspecified number of ♂.

One ♂ syntype with labels: "Paramastax facialis Sauss., Sarayacu" [handwritten on green paper]; "Paramastax facialis Sss., Holotypus ♂, C S Carbonell – 1966" [handwritten by Carbonell on red card]; "Type series unspecified: treat as syntype. Hollier 2011" [handwritten on red paper]. Specimen set with right wings spread and left wings folded; most of the right antenna, the tarsi of the left front and middle legs and the last tarsal segment of the left hind leg are lost. Images on OSF. Box S2.

A junior synonym of *Pseudomastax collaris* (Gerstaecker, 1889).

filiformis Saussure, 1861a: 313 [*Proscopia*].

Chili. Unspecified number of ♂.

No specimens found in the MHNG collection. The whereabouts of the type material is unknown.

A junior synonym of *Astroma chloropterum* Charpentier, 1841.

finoti Saussure, 1903b: 106-107 [*Euschmidtia*].

Maroancetra in Madagascar. Unspecified number of ♀.

No specimens found in the MHNG collection. According to OSF there is a ♀ syntype, referred to as the holotype, in the MNHN.

Maroantsetraia finoti (Saussure, 1903).

finoti Saussure, 1903b: 74-75, fig. 5 [*Scirtotypus*].

Gabonia (coll. Finot). Unspecified number of ♀.

No specimens found in the MHNG collection. According to OSF there is a ♀ syntype, referred to as the holotype, in the MNHN, having been in the collection of Finot when the description was published.

A junior synonym of *Hemierianthus gabonicus* Saussure, 1903.

flavipes Saussure, 1903b: 79-80, fig. 10 [*Erianthus*].

Carin-Cheba (Mus. Genavense). One ♀.

Holotype ♀ with labels: "Carin Cheba, 900-1100m, L. Fea V XII.88" [printed on white card]; "Erianthus flavipes Sauss., Carin Cheba" [handwritten on yellow paper]; "Holotypus" [printed on red card]. Specimen set with left wings spread and right wings folded; both antennae, the right front and middle legs, the tarsi of the left middle leg and the last tarsal segment of both hind legs are lost. Box S1.

A junior synonym of *Erianthus versicolor* Brunner von Wattenwyl, 1898.

furcatus Saussure, 1903b: 101, fig. 16 [*Xanthomastax*].

Nova-Guinea. Unspecified number of ♂.

No specimens found in the MHNG collection. According to OSF there is a ♂ syntype, referred to as the holotype, in the HNHM.

Mnesiclesina furcatus (Saussure, 1903).

fusiformis Saussure, 1899: 642-643 [*Caprorhinus*].

Madagascar. Unspecified number of ♂.

No specimens found in the MHNG collection. The type material is in the MNHN according to Dirsh (1963: 72).

Caprorhinus fusiformis Saussure, 1899.

gabonicus Saussure, 1903a: 412-413 [*Hemierianthus*].

Gabonia (Mus. Genavense). One ♂.

Holotype ♂ with labels: "Gabon, Mr Ed Sarazin" [handwritten on white card]; "Hemierianthus gabonicus Sauss., Gabon" [handwritten on pink paper]; "Holotypus" [printed on red card]. Specimens set with right wings spread and left wings folded; both antennae (apart from a fragment attached with glue to the face), the tarsi of the right middle leg, the last tarsal segment of the left hind leg and the tarsi of the right hind leg are lost. The abdomen is broken about half way along, and the tip has been glued to the locality label. Box S1.

Hemierianthus gabonicus Saussure, 1903.

gavialis Saussure, 1861b: 485-486 [*Scelymena*].

Ile de Ceylan, Peradenia (leg. Humbert). Unspecified number of ♂ and more than one ♀ (variation to prothorax mentioned).

One ♀ syntype with labels: "Sc. gavialis Sauss., Ceylan, M. Humbert" [handwritten on white paper]; "Syntypus" [printed on red paper]. Specimen set with wings folded. It is possible that other syntypes, which were not labelled as such, have been placed under new names when the collection was rearranged in the early 1930s. Box Q2.

Euscelimena gavialis (Saussure, 1861).

hova Saussure, 1899: 640 [*Atractomorpha*].

Nossi-Bé. Unspecified number of ♂ and ♀.

Lectotype ♀ (designated by Kevan & Chen, 1969: 90) with labels: "Nossi Bé" [handwritten on pink paper]; "♀ LECTOTYPE, Atractomorphus hova Sss, Det. D. K. McE. Kevan, 1957" [handwritten, "♀ LECTOTYPE" in red, on white card with "Det. D. K. McE. Kevan, 195" printed]; "= Atractomorpha acutipennis acutipennis (Guérin) Det. D. K. McE. Kevan, 1958" [handwritten on white card with "Det. D. K. McE. Kevan, 195" printed]. Specimens set with wings folded; most of both antennae, both middle legs and the right hind leg are lost. There is also a ♂ paralectotype. Banerjee & Kevan (1960: 183) mention a lectotype for this species, but do not state which specimen is referred to. Kevan (1977: 363) designated this lectotype as the neotype of *A. acutipennis acutipennis* (Guérin-Méneville). Box X4.

A junior synonym of *Atractomorpha acutipennis acutipennis* (Guérin-Méneville, 1844).

hova Saussure, 1903b: 104-105 [*Euschmidtia*].

Madagascar (Mus. Genavense). One ♂ and three ♀.

Lectotype ♂ (designated by Descamps, 1964: 116) with labels: "H. de Saussure, Madagascar" [printed on white paper]; "Euschmidtia hova Sauss.,

Madagascar ♂ [handwritten on pink paper]; "TYPE" [printed on red paper]; "Lobomastax hova (Sauss 1903), Descamps det." [handwritten by Descamps on white card]; "Lectotypus" [printed on red card]. Specimen lacks most of both antennae, the left hind leg and the tarsi of the right hind leg. There are also two ♀ paralectotypes. Box S3.

Lobomastax hova (Saussure, 1903).

hova Saussure, 1899: 643-644 [*Zonocerus*].

Madagaskar. Unspecified number of ♀.

One ♂ syntype with labels: "Zonocerus Hova ♂ Sss." [handwritten on white paper]; "Type" [printed on white card disk with red border]; "Zonocerus hova Sauss., Type!, = Zon. elegans Thunb., V. M. Dirsh det. 1958" [handwritten on white card with "V. M. Dirsh det. 195" printed]. The species name label in the insect box has the locality "Madagascar" handwritten in the lower left corner. The specimen lacks the claws of the left front leg and the last tarsal segment of the left middle leg. While the original description states that the material seen by Saussure was ♀, the measurements of the specimen conform to those given in the description, suggesting that this was a lapse (see Dirsh, 1961: 396). However, it is also possible that there is a ♀ type in the SMFD. Box X9.

A junior synonym of *Zonocerus elegans elegans* (Thunberg, 1815).

humbertianus Saussure, 1861b: 478 [*Cladonotus*].

Ile de Ceylan, Trincomalie & Peradinia (leg. Humbert). More than one ♂ (variability of the spines and tubercles mentioned).

One ♂ syntype with labels: "Ceylon, Humbert" [handwritten on yellow paper]; "Cladonotus Humbertianus Sauss." [handwritten on yellow paper]; "24. Cladonotus Humbertianus Sss., Bolivar vidit." [handwritten on white paper]; "Syntypus" [printed on red paper]. Specimen lacks the antennae, two tarsal segments of the left middle leg, the tibia and tarsi of the right middle leg and the last tarsal segment of the right hind leg. Box Q1.

Cladonotus humbertianus Saussure, 1861.

humbertianus Saussure, 1903b: 83-84, fig. 9 [*Erianthus*].

Ceylon (Mus. Genavense, Humbert). One ♀.

Holotype ♀ with labels: "Erianthus Humbertianus Sauss., Ceylon (Humbert)" [handwritten on yellow paper]; "Holotypus" [printed on red card]: Specimen set with right wings spread and left wings folded; both antennae, the tarsi of the right front leg, the tarsi of the left middle leg and the last tarsal segment of both hind legs are missing. Box S1.

Burrinia humbertiana (Saussure, 1903).

lobipennis Saussure, 1903b: 109-110, fig. 17 [*Euschmidtia*].

Madagascar, Maroancetra (coll. Finot). Unspecified number of ♀.

No specimens found in the MHNG collection. The ♀ lectotype (designated by Decamps, 1964: 168) is in the MNHN.

Pseudoschmidtia lobipennis (Saussure, 1903).

meridionalis Saussure in Distant, 1892: 262, pl. IV, fig. 5 [*Chrotogonus*].

Zoutpansberg. Unspecified number of ♀.

No specimens found in the MHNG collection. There is a ♀ syntype, referred to as the holotype on OSF, in the BMNH.

A junior synonym of *Chrotogonus hemipterus* Schaum, 1853.

mexicana Saussure, 1861a: 400 [*Tettix*].

Mexico calida. Unspecified number of ♂ and ♀.

Lectotype ♀ (designated by Rehn & Grant, 1957: 277) with labels: "Tampico, t.c." [printed on white card]; "Paratettix mexicanus Sauss." [handwritten on green paper]; "Musée de Genève, Paratettix mexicana" [determination handwritten on printed white card]; "Tettix mexicanus Sauss., TYPE, selected by Rehn and Grant" [handwritten on red card with "TYPE" printed]. Specimen set with wings roughly folded, the left hind wing projecting somewhat; both antennae and the tarsi of the right middle leg are lost. There are also two paralectotypes. Box Q5.

Paratettix mexicanus (Saussure, 1861).

mexicanum Saussure, 1859: 390-391 [*Ichthydion*].

Mexico calida. Unspecified number of ♂ and ♀.

Lectotype ♂ (designated by Kevan, Singh & Akbar, 1964: 263) with labels: "Ichthydion mexicanum Sss., 13 ♂" [handwritten on bluish paper]; "Ichthydion mexicanum Sauss." [handwritten on green paper]; "Ichthydion [sic] mexicanum Sss, LECTOTYPE, Det. D.K.McE. Kevan, 19561" [handwritten on white card with "Det. D.K.McE. Kevan, 195" printed]. The species name label in the insect box has the locality "Mexique" handwritten in the lower left corner. Specimen lacks the left antenna, two tarsal segments of the left front leg, part of the tibia and the tarsi of the right front leg, part of the tibia and the tarsi of the right middle leg and the left hind leg. There are also two ♂ and three ♀ paralectotypes. Images on OSF. Box X6.

Ichthyotettix mexicanus (Saussure, 1859).

mexicanum Saussure, 1859: 390 [*Sphenarium*].

Mexico calida. Unspecified number of ♂ and ♀.

Lectotype ♀ (designated by Kevan, 1977: 420) with labels: "Mexiq." [printed on white card]; "Sph. mexicanum Sauss." [handwritten on green paper]; "LECTOTYPE, Det. D.K.McE. Kevan, 19560" [handwritten on white card with "Det. D.K.McE. Kevan, 195" printed]. Specimen lacks both antennae. In the designation Kevan refers to the lectotype as ♂. There are also four ♂ and six ♀ paralectotypes. Images on OSF. Box X6.

Sphenarium mexicanum mexicanum Saussure, 1859.

nasutus Saussure, 1899: 638-639, figs 36-37 [*Geloius*].

Madagaskar. Unspecified number of ♂ and ♀.

Lectotype ♀ (designated by Dirsh, 1961: 397) with labels: "Madagask., Grandid." [handwritten on white paper]; "Geloius nasutus Sss, ♀" [handwritten on white paper]; "Geloius nasutus Sauss." [handwritten on white paper]; "Type" [printed

on white card disk with red margin]; “*Geloius nasutus* Sss Type” [handwritten on white card]; “*Lectotypus*” [printed on red card]. Specimen lacks the right antenna. The original description treated both sexes and there are presumably paralectotypes in the SMFD. Box X16.

Geloius nasutus Saussure, 1899.

nebulosus Saussure, 1903b: 86 [*Erucius*].

Borneo, Provincia Brunnei [sic]. One ♀.

Holotype ♀ with labels: “Brunnei, E Borneo, Fruhstorfer” [printed on yellow paper]; “*Erucius nebulosus* Sauss., Borneo ♀” [handwritten on yellow paper]; “*Holotypus*” [printed on red card]. Specimen set with wings spread; the antennae and the left hind leg are missing. The right hind leg and most of the abdomen are detached and glued to a card on the original pin, the right femur is broken, the proximal part being glued to the abdomen. The abdomen and thorax have been hollowed out by insect feeding. Box S1.

A junior synonym of *Erucius pictus* Saussure, 1903.

parvipennis Saussure, 1903b: 108 [*Euschmidtia*].

Maroancetra in Madagascar (coll. Finot). Unspecified number of ♀.

No specimens found in the MHNG collection. There is a ♀ syntype from Finot's collection, referred to as the holotype on OSF, in the MNHN.

Pseudoschmidtia parvipennis (Saussure, 1903).

pictus Saussure, 1903b: 85-86, fig. 13 [*Erucius*].

Borneo, Nanza-Badan. One ♂.

No specimens found in the MHNG collection. The original description does not state where the ♂ holotype was deposited and its current whereabouts is unknown.

Erucius pictus Saussure, 1903.

rostrata Saussure, 1899: 644, 645 [*Taphronota*].

Africa tropicalis, Camerun. Unspecified number of ♂ and ♀.

Lectotype ♀ (designated by Kevan, 1975: 109) with labels: “CAMERUN” [printed on pink paper]; “*Taphronota rostrata* Sss” [handwritten on pink paper]; “Lectotype of *Taphronota rostrata* Sss. = *T. occidentalis* Kach., Det. D.K.McE. KEVAN. 1956” [handwritten on white card with “Det. D.K.McE. KEVAN. 195” printed]; “*Lectotypus*” [printed on red card]. Specimen set with left wings spread and right wings folded; the last tarsal segments of both front legs, the tarsi of the left middle leg, the claw of the right hind leg and the entire left hind leg are missing. There are two ♂ paralectotypes with the same data labels. Box X13.

A junior synonym of *Taphronota occidentalis* Karsch, 1892.

sakalava Saussure, 1903b: 107-108 [*Euschmidtia*].

Madagascar (Mus. Genavensis, Sikora). Unspecified number of ♀.

One ♀ syntype with labels: “H. de Saussure, Madagascar” [printed on white paper]; “*Euschmidtia sakalava* Sauss., Madagascar ♀” [handwritten on pink paper];

“Holotypus” [printed on red card]; “Type series unspecified: treat as syntype. Hollier 2011” [handwritten on red paper]. Specimen lacks the left antenna, the last tarsal segment of the left front leg and the claws of both hind legs. Box S3.

Pseudoschmidtia sakalava (Saussure, 1903).

saltator Saussure, 1903b: 88 [*Parepisactus*].

Costa-Rica; Guatemala (Mus. Genavense, Rodriguez). Three ♀.

One ♀ syntype with labels: “Guatemala, Rodriguez” [printed on green card]; “di Borre” [handwritten on white card]; “*Parepisactus saltator*, Guatemala-Rodrig. Sauss” [handwritten on green paper]; “*Parepisactus saltator* Sss., Hololectotypus [sic] ♀, C S Carbonell - 1966” [handwritten by Carbonell on red card]. Specimen lacks both antennae, the left front leg, the tarsi of the right front leg, both middle legs and the tarsi of both hind legs. There is a second ♀ labelled “COSTA RICA” [printed on a strip of green paper] which may be a syntype, although Carbonell (in lit.) noted that it may not be con-specific. The lectotype has not been formally designated. Images on OSF. Box S2.

Parepisactus saltator Saussure, 1903.

savignyi Saussure, 1889: 89-90 [*Leptoscirtus*].

Aegyptus. Unspecified number of ♀.

No specimens found in the MHNG. The species was described from an illustration in Savigny (1817: Orthoptera plate 6, figure 1) and the type is presumably in the MNHN.

A junior synonym of *Tenuitarsus angustus* (Blanchard, 1836).

sibiricus Saussure in Bolivar 1887: 265 [*Tettix*].

Siberia orientale (Mus. Genève). Unspecified number of ♀.

Five ♀ syntypes. A ♀ with labels: “SIBERIE 1” [locality printed, numeral handwritten in red ink, on white card]; “*Tettix sibiricus* Sss., Sibir” [handwritten on white paper]; “Syntypus” [printed on red paper]. A ♀ with labels: “SIBERIE 1” [locality printed, numeral handwritten in red ink, on white card]; “*Tettix sibiricus* Sauss.” [handwritten on blue paper]; “Syntypus” [printed on red paper]. Specimen lacks both antennae, the tarsi of the right middle leg and the claw of the left hind leg. A ♀ with labels: “SIBERIE 1” [locality printed, numeral handwritten in red ink, on white card]; “*Tettix sibiricus* Ss.” [handwritten on blue paper]; “Syntypus” [printed on red paper]. Specimen lacks two tarsal segments of the left hind leg. A ♀ with labels: “SIBERIE 1” [locality printed, numeral handwritten in red ink, on white card]; “*Tettix sibiricus* Ss.” [handwritten on blue paper]; “Syntypus” [printed on red paper]. A ♀ with labels: “SIBERIE” [printed on white card]; “*Tettix sibiricus* Sauss.” [handwritten on blue paper]; “Syntypus” [printed on red paper]. Specimen lacks the right antenna and the claw of the right front leg. There are a further five specimens labelled “KAMTECHAKA” placed under this name which could be syntypes. Box Q6.

A junior synonym of *Tettix japonica* (Bolivar, 1887).

squalinus Saussure, 1899: 641, fig. 38 [*Dyscolorhinus*].

Madagascar. More than one ♀.

Lectotype ♀ (designated by Dirsh, 1961: 397) with labels: “Madagasc, Tananarive” [printed on pink paper]; “Dyscolorhinus squalinus Sauss.” [handwritten on pink paper]; “Type” [printed on white card disk with red border]; “LECTO-TYPE” [handwritten on white paper]; “Dyscolorhinus squalinus Sauss., V. M. Dirsh det. 1958, Type!” [handwritten on white card with “V. M. Dirsh det. 195” printed]; “LECTO-TYPE designated Dirsh 1961” [handwritten on red paper]. Specimen lacks the tarsi of the left front leg and the right hind leg. There are six ♂ and fourteen ♀ specimens with similar data which could be paralectotypes. Box X6.

Dyscolorhinus squalinus Saussure, 1899.

squalinus Saussure in Bolivar, 1884: 423 [*Pyrgomorpha*].

India (coll. Brunner n° 12749). Unspecified number of ♀.

Amongst the material in the MHNG collection are five ♂ and seven ♀ specimens with Saussure's labels accompanied by a note “Part of series from which type was described, D. K. K. 1969” [handwritten by Kevan on white card]. In the original description the type material is stated to be in the collection of Brunner von Wattenwyl, but comparison of the specimen he considered to be the holotype and the material in the MHNG led Kevan (1970: 856) to conclude that Brunner's specimen had come from Saussure's collection. It is unlikely, however, that Bolivar saw the material now in the MHNG collection when preparing the description. Kevan (1970: 853) states that the holotype is in the NHMW. Box X4.

Zarytes squalinus squalinus (Saussure, 1884).

subverrucosa Saussure, 1899: 645, 646 [*Taphronota*].

Africa tropicalis, specimina decolorata. More than one ♂.

One ♂ syntype with labels: “Taphronota subverrucosa Sauss.” [handwritten on pink paper]; “Holotype of Taphronota subverrucosa Sss, Det. D.K.McE. Kevan, 1956” [handwritten on white card with “Det. D.K.McE. Kevan, 195” printed]; “Syntype not holotype, Hollier 2012. The species name label in the insect box has the locality “Afriq. trop.” handwritten in the lower left corner. Specimen set with wings spread; part of the left antenna is missing. Box X13.

A junior synonym of *Taphronota ferruginea ferruginea* (Fabricius, 1781).

sulcata Saussure, 1903b: 59-61 [*Phyllochoreia*].

India (BMNH). One damaged ♀.

No specimens found in the MHNG collection. The holotype was in the BMNH when the description was published but does not appear on their online database.

A junior synonym of *Phyllochoreia unicolor* Westwood, 1839.

taeniata Saussure, 1903b: 96-97 [*Paramastax*].

Brasilia (Mus. Genavense). Unspecified number of ♂.

One ♂ syntype with labels: “Brésil” [handwritten on white paper]; “Paramastax taeniata Sauss., Brésil” [handwritten on green paper]; “Paramastax Taeniata Sss., Holotypus ♂, C S Carbonell, 1966” [handwritten by Carbonell on red card]. Specimen set with wings spread, these are very ragged; the antennae, the tibia and tarsi of the left

front leg, the tarsi of the right front leg, most of the femur, the tibia and tarsi of the right middle leg, the tarsi of the left hind leg and the right hind leg are lost. There is considerable insect feeding-damage to the thorax and abdomen. This specimen is referred to as the holotype by Descamps (1973: 959) without comment. Images on OSF. Box S2.

Pseudomastax taeniata (Saussure, 1903).

tartarus Saussure in Bolivar, 1887: 262-263 [*Tettix*].

Turkestan. Unspecified number of ♂ and ♀ (variation to the pronotum mentioned).

Two ♂ and three ♀ possible syntypes. A ♂ with labels: "2" [handwritten on white paper]; "Vallée du Sarafshan" [handwritten on white paper]; "Tettix tartarus var. Sauss." [handwritten on blue paper]. Specimen lacks the left hind leg. A ♂ with labels: "Tashkent" [printed in Cyrillic characters on a strip of white paper]; "Tettix tartarus Sauss." [handwritten on blue paper]. A ♀ with labels: "tartarus Ss. var., Turkestan, M.H.S." [handwritten on white paper]; "Tettix tartarus Sauss." [handwritten on blue paper]. A ♀ with labels: "Tashkent" [printed in Cyrillic characters on a strip of white paper]; "Tettix tartarus Sauss." [handwritten on blue paper]. Specimen lacks both antennae, the tarsi of the left front leg, the tibia and tarsi of the right front leg and the tarsi of the right middle leg. A ♀ with labels: "4" [printed on white card with a red line]; "Tashkent" [printed in Cyrillic characters on a strip of white paper]; "tartarus Ss. var., Turkestan, M.H.S." [handwritten on white paper] "Tettix tartarus Sauss." [handwritten on blue paper]. Specimen lacks the left antenna and the right hind leg. There are several more specimens without locality labels. This species was described on the basis of material given to Bolivar by Saussure. It is not clear from the original description whether Bolivar only saw the material he kept in his collection. According to OSF there are only ♂ syntypes in the MNMS, so it is probable that some of the specimens in the MHNG are syntypes. Box Q6.

Tetrix tartara tartara (Saussure in Bolívar, 1887).

testudo Saussure, 1861a: 402 [*Amorphopus*].

Guyana. Unspecified.

No specimens found in the MHNG collection. The whereabouts of the type material is unknown.

Amorphopus testuda Saussure, 1861.

tolteca Saussure, 1861a: 401 [*Tettix*].

Mexico calida. Unspecified number of ♂ and ♀.

Lectotype ♂ (designated by Rehn & Grant, 1957: 312) with labels: "Tampico. t.c." [printed on white card]; "Paratettix tolteca Sauss." [handwritten on green paper]; "Musée de Genève, Paratettix tolteca S." [determination handwritten on printed white card]; "Tettix tolteca Sauss., selected by Rehn and Grant, TYPE" [handwritten on red card with "TYPE" printed]. Specimen lacks both antennae, both front legs, the tarsi of the left middle leg, the tibia and tarsi of the right middle leg and the tibia and tarsi of the right hind leg. There is at least one paralectotype with the same data. Box Q6.

Paratettix toltecus (Saussure, 1861).

vaginalis Saussure, 1903b: 87 [*Mastacides*].

Montes Kodikam in India meridionali (coll. Finot). More than one ♀.

No specimens found in the MHNG collection. The type material was in the collection of Finot when the description was published and is now in the MNHN according to OSF.

A junior synonym of *Mastacides pupaeformis* Bolivar, 1899.

versicolor Saussure, 1903b: 108-109 [*Euschmidia*].

Madagascar, Maroancetra (coll. Finot). Unspecified number of ♂.

No specimens found in the MHNG collection. The ♂ lectotype (designated by Descamps, 1964: 143) is in the MNHN, having been in the collection of Finot when the description was published.

Pseudoschmidia versicolor (Saussure, 1903).

voeltzkowiana Saussure, 1899: 656-657 [*Paratettix*].

Nossi-Bé. Unspecified number of ♂ and more than one ♀.

One ♂ and two ♀ syntypes. A ♂ with labels: "Nosi bé" [handwritten on pink paper]; "♂" [printed on white paper]; "Paratettix voeltzkowiana Sauss." [handwritten on pink paper]; "Syntypus" [printed on red paper]. Specimen set with wings roughly folded; the tarsi of the right middle leg are lost. A ♀ with labels: "Nosi bé" [handwritten on pink paper]; "♀" [printed on white paper]; "Paratettix voeltzkowiana Sauss." [handwritten on pink paper]; "Syntypus" [printed on red paper]. Specimen set with wings roughly folded. A ♀ with labels: "Nosi bé" [handwritten on pink paper]; "♀" [printed on white paper]; "Paratettix voeltzkowiana Sauss." [handwritten on pink paper]; "Syntypus" [printed on red paper]. Specimen set with wings folded; both antennae are missing. There are another six ♂ and eleven ♀ specimens with different locality labels which are probably not syntypes. Box Q5.

Morphopoides voeltzkowiana (Saussure, 1899). Considered a *nomen dubium* on OSF.

ACKNOWLEDGEMENTS

Thanks are due to Anita Hollier, Peter Schwendinger and Bernhard Merz for comments on the layout and text, and to Bernd Hauser for historical information about the MHNG collection. Special thanks are due to Carlos Carbonell, who made available his notes on the MHNG collection. Harald Bruckner kindly provided information about the holdings of the NHMW and Val McAtear supplied some literature from the Royal Entomological Society library.

REFERENCES

- BANERJEE, S. K. & KEVAN, D. K. M. 1960. A preliminary revision of the genus *Atractomorpha* Saussure, 1862 (Orthoptera : Acridioidea : Pyrgomorphidae). *Treubia* 25: 165-189.
- BOLÍVAR, I. 1884. Monografía de los pirgomorfinos. *Anales de la Sociedad Española de Historia Natural* 13: 1-73, 418-500.
- BOLÍVAR, I. 1887. Essai sur les Acridiens de la tribu des Tettigidae. *Annales de la Société Entomologique de Belgique* 31: 175-313.

- DESCAMPS, M. 1964. Révision préliminaire des Euschmidtinae (Orthoptera - Eumastacidae). *Mémoires du Muséum national d'histoire naturelle* (Série A, Zoologie) 30: 1-324.
- DESCAMPS, M. 1965. Contribution à l'étude des Eumastacides Malgaches (Orthoptera - Eumastacidae). I. Révision des Miraculinae. *Mémoires du Muséum national d'histoire naturelle* (Série A, Zoologie) 34: 3-57.
- DESCAMPS, M. 1970. Révision des Pseudomastacinae (Orth., Eumastacidae). *Annales de la Société Entomologique de France* 6: 613-635.
- DESCAMPS, M. 1973. Diagnosis et signalisations d'Eumastacoidea (Orth.). IV. Amérique. *Annales de la Société Entomologique de France* (N.S.) 9: 943-974.
- DIRSH, V. M. 1961. Notes on Acridoidea of Africa, Madagascar and Asia (Orthoptera). *Eos, Revista española de Entomología* 37: 379-398.
- DIRSH, V. M. 1963. The Acridoidea (Orthoptera) of Madagascar III. Pyrgomorphidae. *Bulletin of the British Museum (Natural History) Entomology* 13: 51-103.
- DIRSH, V. M. & MASON, J. B. 1979. Systematic and phylogenetic position of the family Xyronotidae (Acridomorpha, Insecta). *Zeitschrift für zoologische Systematik und Evolutionforschung* 17: 201-210.
- DISTANT, W. L. 1892. A naturalist in the Transvaal. *R. H. Porter, London*. xiv + 277 pp.
- EADES, D. C., OTTE, D., CIGLIANO, M. M. & BRAUN, H. 2012. *Orthoptera Species File Online*. Version 2.0/4.0. <http://www.Orthoptera.SpeciesFile.org> [accessed 20.xi.2012].
- HOLLIER, J. 2012a. An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève, Part 2: The Acrididae: Oedipodinae. *Revue suisse de Zoologie* 119: 215-260.
- HOLLIER, J. 2012b. An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève, Part 3: The Acrididoidea excluding the Acrididae: Oedipodinae. *Revue suisse de Zoologie* 119: 303-339.
- HOLLIER, J. & HEADS, S. M. 2012. An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève, Part 1: The Tridactyloidea. *Revue suisse de Zoologie* 119: 149-160.
- KEVAN, D. K. M. 1952. On the systematic position of two anomalous genera previously placed in the subfamily Pyrgomorphinae (Orth., Acrididae). *Entomologist's monthly Magazine* 88: 265-272.
- KEVAN, D. K. M. 1960. On the identity of *Minorissa alata* Thomas, 1874, and *Atractomorpha congensis* Saussure, 1893 [nomen nudum] (Orthoptera: Pyrgomorphidae). *Bulletin of the Brooklyn Entomological Society* 55: 36-41.
- KEVAN, D. K. M. 1963. Pyrgomorphidae (Orthoptera; Acridoidea) in the collection of C. P. Thunberg, Uppsala, with notes on type material of the species represented. *Arkiv för Zoologi* 16: 69-94.
- KEVAN, D. K. M. 1970. Indian Pyrgomorphini other than *Pyrgomorpha*. *Revue suisse de Zoologie* 77: 851-866.
- KEVAN, D. K. M. 1975. A revision of the genus *Taphronota* Stål 1873 (Orthoptera: Acridoidea, Pyrgomorphidae). *Publicações Culturais da Companhia de Diamantes de Angola* 88: 79-149.
- KEVAN, D. K. M. 1977. Superfamily Acridoidea, fam. Pyrgomorphidae. In: BEIER, M. (ed.). *Orthopterorum Catalogus* 16: 1-656.
- KEVAN, D. K. M. & CHEN, Y. K. 1969. A revised synopsis of the genus *Atractomorpha* Saussure, 1862 (Orthoptera: Pyrgomorphidae) with an account of the African aberrans-group. *Zoological Journal of the Linnean Society* 48: 141-198.
- KEVAN, D. K. M., SINGH, A. & AKBAR, S. 1964. A revision of the Mexican Pyrgomorphidae (Orthoptera: Acridoidea). I. Genera other than *Sphenarium*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 116: 231-298.

- OHL, M. & OSWALD, J. D. 2004. Annotated list of the primary type specimens of Megaloptera and Raphidioptera (Insecta, Neuropterida) in the Museum für Naturkunde der Humboldt-Universität zu Berlin. *Deutsche Entomologische Zeitschrift* (N.S.) 51: 87-96.
- REHN, J. A. G. & GRANT, H. J. 1957. The genus *Paratettix* as found in North America (Orthoptera; Acridoidea; Tetrigidae). *Proceedings of the Academy of Natural Sciences of Philadelphia* 109: 247-319.
- RILEY, C.V. 1893. Scientific results of the U. S. Eclipse expedition to West Africa 1889-'90. Report upon the Insecta, Arachnida and Myriopoda. *Proceedings of the United States National Museum* 16: 565-590.
- SAUSSURE, H. DE 1859. Orthoptera Nova Americana. *Revue et Magasin de Zoologie Pure et Appliquée* 11: 201-212, 315-316, 390-394.
- SAUSSURE, H. DE 1861a. Orthoptera Nova Americana. *Revue et Magasin de Zoologie Pure et Appliquée* 13: 126-130, 156-164, 313-324, 397-402.
- SAUSSURE, H. DE 1861b. Etudes sur quelques Orthoptères du Musée de Genève. *Annales de la Société Entomologique de France* (4th series) 1: 469-494.
- SAUSSURE, H. DE 1884. Prodromus Oedipodiorum, Insectorum ex ordine Orthopterorum. *Mémoires de la Société de Physique et d'Histoire naturelle de Genève* 28(9): 1-258.
- SAUSSURE, H. DE 1899. Orthoptera (pp. 567-664). In: VOELTZKOW, A. (ed.). Wissenschaftliche Ergebnisse der Reisen in Madagaskar und Ostafrika in den Jahren 1889-95. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 21: 1-664.
- SAUSSURE, H. DE 1903a. Diagnosen von 4 neuen Gattungen der Eumastaciden (Orthoptera: Acridoidea). *Zoologischer Anzeiger* 26: 412-415. (Appeared 8.v.1903).
- SAUSSURE, H. DE 1903b. Analecta entomologica II. Notice sur la tribu des Eumastaciens. *Revue suisse de Zoologie* 11: 43-114. (Appeared 1.vii.1903).
- SAVIGNY, J.-C. 1817. Description de l'Égypte: ou recueil des observations et des recherches qui ont été faites en Égypte. Publié par les ordres de sa majesté l'empereur Napoléon le Grand. Histoire naturelle. Volume 19. Histoire Naturelle: Planches II. *Imprimerie nationale, Paris*, 212 pp.
- WILLEMSE, C. J. M. 1931. Orthoptera Celebica Sarasiniana. I. Saltatoria, Fam. Acrididae. *Treubia* 12: 189-270.

The Embioptera (Insecta) described by Henri de Saussure

John HOLLIER

Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Switzerland.

Email: john.hollier@ville-ge.ch

The Embioptera (Insecta) described by Henri de Saussure. - The seven species of Embioptera described by Saussure are listed alphabetically and details of the type specimens held in the collection of the Muséum d'histoire naturelle de Genève are given, along with the current taxonomic status of the species.

Keywords: Embiidina - Anisembiidae - Archembiidae - Clothodidae - Embiidae - Oligotomidae - type-catalogue - Geneva Museum.

INTRODUCTION

Henri de Saussure (1828-1905) was an important and prolific entomologist specialising in the Hymenoptera and the Orthoptera (*sensu lato*). Details of his career are given in Hollier & Heads (2012). The Embioptera holdings of the Muséum d'histoire naturelle de Genève (MHNG) are very small, but include the type specimens of the seven species described by Saussure in two publications. The dating of Saussure's two publications is potentially problematic because both appeared in the same year and two of the species are described as new in both, with a difference in spelling in one case. Davis (1939b) states that the paper in the Journal of the Trinidad Field Naturalist Club (Saussure, 1896a) was published in February, whilst that in the Mitteilungen der Schweizerische entomologische Gesellschaft (Saussure, 1896b) was published in July. The latter has the month printed on the fascicle containing Saussure's paper, and the Secretary of the Trinidad and Tobago Field Naturalist's Club kindly confirmed the publication date of their Journal (Gomes, pers. comm.). The orthography of those names occurring in both papers therefore follows Saussure, 1896a.

Saussure did not nominate holotypes in his descriptions, and did not always mention the number of specimens he had, so unless it is clear from the description that only one was available to him the specimens are treated as syntypes.

Saussure's specimens were studied by Herman Krauss (1848-1939) and illustrated in his monograph on the group (Krauss, 1911).

Harold Consett Davis (1913-1944) did not see these specimens, but corresponded with Jean Carl (then curator of arthropods) in 1938-1939 (letters in the MHNG archive). Carl made drawings of some prepared specimens for him because Davis (in a letter to Carl in 1939) stated that he did not consider Krauss' illustrations of the dried specimens sufficient for accurate determination. In return, Davis sent paratypes of four species that he had described from Australia (of which he was a native) to the MHNG. Davis was killed in action in New Guinea during the Second World War.

Saussure's specimens were revised by Edward Ross in the late 1950s, and it appears that he prepared or remounted the specimens to make the slide preparations now in the MHNG collection, the red labels indicating type status being in the same handwriting as some of his determination labels on other specimens. One slide is labelled as a lectotype, but does not seem to have been formally designated as such.

The nomenclature of the Embioptera (even the name of the order) is rather confused. The last works to treat the whole group being Krauss (1911) and Enderlein (1912). Miller (2009) has attempted to resolve the problems for family- and genus-level names, but the two online resources, Maehr & Eades (2012) and Ross (2009), differ both from Miller and each other.

ARRANGEMENT AND FORMAT

Catalogue entries are listed alphabetically by specific epithet and are arranged according to the following format:

specific epithet Author, year: page [*original generic placement*].

Type locality as given in the original description. Type series.

Number of specimens. Specimen: "Label data" [format of label]. Following the recommendations of Ohl & Oswald (2004) the condition of each specimen is noted. Other comments and a discussion of the nomenclature.

At the period Saussure described his species there were no family divisions in the Embioptera (Saussure regarded the group as a tribe) and all of his species are in the same genus. To make the relationships of the species clearer the family has been given with the current combination (following Miller, 2009).

CATALOGUE

bramina Saussure, 1896b: 352 [*Embia*].

India orientalis: Bombay [sic]. Unspecified number of ♂.

One slide-mounted ♂ syntype with the labels: "1 5 Bombay, Indes Or., Hi de Saussure" [handwritten on white card]; "*Embia brahmia* [sic] Sss." [handwritten on yellow paper]; "EMBIA BRAMINA SAUSS: TYPE" [handwritten on red card]. The first two labels have holes indicating that they were originally placed on an insect pin. The slide has two cover slips: the first covers two forewings and one hind wing; the second covers the cleared but intact body of the specimen. The left front and right middle legs are lost, as is one of the wings, and part of the base of the abdomen is missing. The right front, left middle and left hind legs are detached from the specimen.

Ross (2009) considers this name to be a junior synonym of *Oligotoma saundersii* (Westwood, 1837).

Oligotomidae: *Oligotoma bramina* (Saussure, 1896).

hova Saussure, 1896b: 354-355, fig. 14 [*Embia*].

Madagascar. Unspecified number of ♂ and ♀.

A slide-mounted ♂ syntype with labels: "Madagascar, M^r de Saussure" [handwritten on pink paper]; "*Embia spec.*" [handwritten on pink paper]; "O. *hova* Sauss.

♂" [handwritten on white paper]; "EMBIA HOVA SAUSS: ♂ LECTOTYPE" [handwritten on red card]. The first three labels have holes indicating that they were originally placed on an insect pin. The slide has two cover slips: the first covers the right fore and hind wings; the second covers the cleared body, which is coming apart between the second and third thoracic segments. Both middle legs are detached and the left forewing is absent, although this might be the detached wing glued to a clear mount on a separate pin with the label: "O. hova Sauss. ♂ Flügel" [handwritten on white paper] in the insect box. The lectotype does not seem to have been formally designated. A ♂ syntype pinned through the thorax with labels: "Madagascar, M^r de Saussure" [handwritten on pink paper]; "O. hova Sauss. ♂" [handwritten on white paper]; "OLIGOTOMA SAUNDERSII (WESTW.) DT ROSS" [handwritten on white card]; "Syntypus" [printed on red paper]. The specimen is set with wings folded; part of the left antenna is missing. A ♂ syntype pinned through the thorax with labels: "Madagascar, M^r de Saussure" [handwritten on pink paper]; "Embica hova Sauss. Cotype, Madagascar" [handwritten by Ross on white paper]; "OLIGOTOMA SAUNDERSII (WESTW.) DT ROSS" [handwritten on white card]; "Syntypus" [printed on red paper]. Specimen set with wings roughly folded; the left hind wing is detached but adheres to the left forewing. A ♂ syntype pinned through the thorax with labels: "Madagascar, M^r de Saussure" [handwritten on pink paper]; "OLIGOTOMA SAUNDERSII (WESTW.) DT ROSS" [handwritten on white card]; "Syntypus" [printed on red paper]. Specimen set with wings roughly folded; the right forewing and right middle leg are missing. A ♂ [?] syntype pinned through the thorax with labels: "Madagascar, M^r de Saussure" [handwritten on pink paper]; "OLIGOTOMA SAUNDERSII (WESTW.) DT ROSS" [handwritten on white card]; "Syntypus" [printed on red paper]. Specimen set with wings folded; most of the left antenna, the right middle leg, both hind legs and the abdomen are missing. This specimen is probably a ♂, being of the same size as the other pinned specimens. No ♀ syntypes are present, although the ♀ characters are mentioned in the original description.

Ross (2009) considers this name to be a junior synonym of *Oligotoma saundersii* (Westwood, 1837).

Oligotomidae: *Oligotoma hova* (Saussure, 1896).

humbertiana Saussure, 1896b: 353-354 [*Embica*].

Ceylon (leg. A. Humbert). One ♂.

Slide-mounted ♂ holotype with labels: "600 81, Ceylan, Voy. Humbert" [handwritten on ruled white card]; "242" [handwritten on white paper]; "Embica humbertiana Sauss." [handwritten on yellow paper]; "EMBIA HUMBERTIANA SAUSS: ♂ TYPE" [handwritten on red card]. The first three labels have holes indicating that they were originally placed on an insect pin. The slide has two cover slips: the first covers the left fore and hind wings; the second, the cleared body of the specimen, which has broken in two between the second and third thoracic segments. Most of the right antenna and both hind legs are lost. Saussure mentioned a second ♂ collected by Humbert in Ceylon at the same time as the specimen described, but this comes after the description and he refers to its differences from the first specimen meaning that it should not be considered a syntype. The second specimen is apparently lost.

Oligotomidae: *Oligotoma humbertiana* (Saussure, 1896).

ruficollis Saussure, 1896b: 353 [*Embia*].

America centralis. One ♂.

Slide-mounted ♂ holotype with labels: "Bugaba, 800-1500 ft., Champion" [printed on white card]; "Embia ruficollis Sss." [handwritten on green paper]; "EMBIA RUFICOLLIS SAUSS: HOLOTYPE" [handwritten on red card]. The first two labels have holes indicating that they were originally placed on an insect pin. The slide has two cover slips: the first covers both pairs of wings; the second covers the cleared but intact body of the specimen. The right antenna is missing and the left middle and hind legs are detached. Ross (1992) mentions that the specimen was originally card-mounted.

Davis (1939a) created the genus *Saussurella* for a specimen mistakenly identified by Longinos Navás as *E. ruficollis* Saussure. Recognising that this genus name was preoccupied, he later proposed the new name *Saussurembia* (Davis, 1940). Ross (1992) considered the generic concept valid, but, having studied the type of *E. ruficollis*, considered the specimen for which it was created to belong to a different species. Ross (1992) placed *ruficollis* Saussure in the genus *Chelicerca*, and described the species used to found the genus *Saussurembia* as *S. davisi*. Miller (2009) stated that in basing the genus on a misidentified specimen Davis is automatically considered to have established a new nominal species, which is the type species for the genus, and made *S. davisi* Ross, 1992 a junior synonym of *S. ruficollis* Davis, 1939. Maehr & Eades (2012) placed both *davisi* Ross and *ruficollis* Davis as distinct species in the genus *Saussurembia*.

Anisembiidae: *Chelicerca ruficollis* (Saussure, 1896).

tartara Saussure, 1896b: 352 [*Embia*].

Turkestan (Mus. Genavense). Unspecified number of ♂.

One slide-mounted ♂ syntype with labels: "600 81 Turkestan, Asie, Anc. coll." [handwritten on ruled white card]; "TURKESTAN, PORTSCHINS" [printed on white card]; "Embia tartara Sss." [handwritten on yellow paper]; "EMBIA TARTARA SAUSS: TYPE" [handwritten on red card]. The first three labels have holes indicating that they were originally placed on an insect pin. The slide has two cover slips: the first covers the left fore and hind wings; the second covers the cleared but intact body of the specimen. The right fore wing and right middle leg are missing, as is part of the right antenna. The left hind leg is under the second coverslip but detached from the thorax.

Davis (1939c: 480) considered that the left cercus was broken rather than one segmented as Saussure had said, and thought that this species was a junior synonym of *Parembia persica* (McLachlan, 1877). In a letter to Carl in 1939 Davis stated that he could not locate the three syntypes of *P. persica* despite having visited the Natural History Museum in London, but the Museum's online database lists slide-mounted type material. Ross (2009) listed this species under *Embia* with a symbol to indicate that the generic combination will be changed.

Embiidae: *Embia tartara* Saussure, 1896.

trinitatis Saussure, 1896a: 293-294 [*Embia*].

Trinidad (leg. Urich). Unspecified number of ♂ and ♀.

A ♂ syntype in alcohol, the vial containing labels: “*Embia trinitatis* Sss. ♂” [handwritten on green paper]; “transféré [sic] de l’essence de girofle en alcool 6.III.1985 B. Hauser” [typewritten on white paper]. The first of these labels has holes indicating that it was originally placed on an insect pin. The jar containing the vial has the labels: “*Rhagadochir trinitatis* (Sauss.)” [typewritten on white card with a green printed margin]; “Syntypus” [printed on red paper]. The specimen is in several pieces: the head and thorax with right front and middle legs and the left hind leg attached; the abdomen; and the left front and middle legs, the right hind leg and all four wings each detached. A ♂ syntype pinned through the thorax with labels: “*Embia trinitatus* Sss. ♂” [handwritten on green paper]; “Syntypus” [printed on red paper]. The specimen is set with wings spread; the hind legs are broken off at the coxae and the abdomen is missing. A ♀ syntype pinned through the thorax with labels: “*Embia trinitatus* Sss. ♀” [handwritten on green paper]; “Syntypus” [printed on red paper]. The left hind leg is missing. A ♀ syntype mounted on a card point with labels: “*Embia trinitatus* Sss. ♀” [handwritten on green paper]; “Syntypus” [printed on red paper]. Most of both antennae and the right hind leg are lost. A ♀ syntype mounted on a card point with labels: “*Embia trinitatus* Sss. ♀” [handwritten on green paper]; “Syntypus” [printed on red paper].

This species was illustrated by Saussure (1896b: figure 13) after the publication of the original description.

Archembiidae: *Pararhagadochir trinitatis* (Saussure, 1896).

urichi Saussure, 1896a: 293 [*Embia*].

Trinidad (leg. Urich). Unspecified number of ♂ and ♀.

A ♂ syntype in alcohol, the vial containing labels: “*Embia uhrichi* Sss. ♂” [handwritten on green paper]; “transféré [sic] de l’essence de girofle en alcool 6.III.1985 B. Hauser” [typewritten on white paper]. The first of these labels has holes indicating that it was originally placed on an insect pin. The jar containing the vial has the labels: “*Antipaluria uhrichi* (Sauss.)” [typewritten on white card with a green printed margin]; “Syntypus” [printed on red paper]. The specimen is in several pieces: the head and part of the thorax with both fore wings, both front legs and the left middle leg attached; part of the thorax and the abdomen with the right hind leg and right hind wing attached; and the left hind wing, right middle leg and left hind leg each detached. The dry specimens lack locality labels but the species name label in the insect box has the locality “Antilles” handwritten in the lower right corner. A ♂ syntype pinned through the thorax with labels: “*Embia uhrichi* Sauss. ♂” [handwritten on green paper]; “Syntypus” [printed on red paper]. Specimen set with wings spread. A ♂ syntype pinned through the thorax with labels: “*Embia uhrichi* Sauss. ♂” [handwritten on green paper]; “Syntypus” [printed on red paper]. Specimen set with wings spread; the right front leg is missing, the left front leg is detached but adheres to the underside of the thorax. A ♂ syntype pinned through the thorax with labels: “*Embia uhrichi* Sauss. ♂” [handwritten on green paper]; “Syntypus” [printed on red paper]. Specimen set with wings spread; the antennae and the left front leg are lost. The left forewing is detached and secured on a separate pin next to the specimen. A ♀ syntype pinned through the thorax with labels: “*Embia uhrichi* Sauss. ♀” [handwritten on green

paper]; "Syntypus" [printed on red paper]. The specimen lacks the left middle leg; the left hind leg is detached and glued to a piece of card secured on the original pin. A ♀ syntype pinned through the thorax with labels: "Embia uhrichi Sauss. ♀" [handwritten on green paper]; "Syntypus" [printed on red paper]. The right front and left hind legs are lost. A ♀ syntype pinned through the thorax with labels: "Embia uhrichi Sauss. ♀" [handwritten on green paper]; "Syntypus" [printed on red paper]. The specimen has suffered extensive insect feeding damage and only part of the thorax with the left middle leg and the tip of the abdomen remain. The left hind leg adheres to the left middle leg. A juvenile ♂ syntype pinned through the thorax with labels: "Embia uhrichi, nymph ♂" [handwritten on green paper]; "Syntypus" [printed on red paper]. The specimen has suffered insect feeding damage and lacks both middle and both hind legs. There is also a detached forewing glued to a clear mount with the labels: "E. uhrichi" [handwritten in pencil on white paper]; "Syntypus" [printed on red paper].

There are many more specimens in alcohol in a second jar and it is unclear whether they should be regarded as syntypes. Saussure (1896b) states that Urich sent him two series of specimens, and that from the second he was able to extract a number of adults in good enough condition to study. It seems reasonable to consider only the specimens which had been pinned and labelled to be syntypes (one of which has subsequently been returned to alcohol), but the specimens in the second jar may be of similar status because it has a label "E. uhrichi" while the raw samples sent by Urich contained a mixture of *A. urichi* and *P. trinitatis*.

This species, including the juvenile ♂, was illustrated by Saussure (1896b: figures 1-12 [figure 5 is labelled 15 on the plate]) after the publication of the original description. The species was named for F. W. Urich, who collected the specimens in Trinidad. For some reason Saussure spelled this "Uhrich" and thus the species became "uhrichi" both in Saussure 1896b and on the specimen labels. In a letter to Carl in 1938 Davis suggests that Urich, who was the editor of the journal in which Saussure 1896a appeared, corrected the spelling at the last minute, leading to the publication of both variants.

Clothodidae: *Antipaluria urichi* (Saussure, 1896).

ACKNOWLEDGEMENTS

Thanks are due to Selwyn Gomes of the Trinidad and Tobago Field Naturalists' Club for confirming the publication date of Saussure's paper and to Val McAtear for providing some of the literature consulted from the Royal Entomological Society library. Christelle Mougin kindly made available the correspondence between Davis and Carl preserved in the MHNG archives, and Bernd Hauser provided some historical information about the MHNG collection. I am also grateful to Anita Hollier for comments on the manuscript.

REFERENCES

- DAVIS, C. 1939a. Taxonomic notes on the Order Embioptera. ii. A new Neotropical genus of Embioptera. *Proceedings of the Linnean Society of New South Wales* 64: 217-222.
- DAVIS, C. 1939b. Taxonomic notes on the Order Embioptera. iv. The genus *Clothoda* Enderlein. *Proceedings of the Linnean Society of New South Wales* 64: 373-380.

- DAVIS, C. 1939c. Taxonomic notes on the Order Embioptera. vi. Three new Asiatic genera related to *Embia* Latreille. *Proceedings of the Linnean Society of New South Wales* 64: 472-482.
- DAVIS, C. 1940. Taxonomic notes on the Order Embioptera. xv. The genus *Rhagadochir* Enderlein and genera convergent to it. *Proceedings of the Linnean Society of New South Wales* 65: 171-191.
- ENDERLEIN, G. 1912. Embiidén. *Catalogue systématique et descriptif des collections zoologiques du Baron Edmond de Selys Longchamps* 3: 1-121.
- HOLLIER, J. & HEADS, S. W. 2012. An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type specimens housed in the Muséum d'histoire naturelle de Genève, Part 1: The Tridactyloidea (Caelifera). *Revue suisse de Zoologie* 119: 149-160.
- KRAUSS, H. A. 1911. Monographie der Embien. *Zoologica* 23 (60): 1-78, 5 plates.
- MAEHR, M. D. & EADES, D. C. 2012. Embioptera Species File Online. Version 1.0/4.1. Available online at <http://Embioptera.SpeciesFile.org> [consulted 16/8/2012].
- MILLER, K. B. 2009. Genus- and family-group names in the order Embioptera (Insecta). *Zootaxa* 2055: 1-34.
- OHL, M. & OSWALD, J. D. 2004. Annotated list of the primary type specimens of Megaloptera and Raphidioptera (Insecta, Neuropterida) in the Museum für Naturkunde der Humboldt-Universität zu Berlin. *Deutsche Entomologische Zeitschrift* (N.S.) 51: 87-96.
- ROSS, E. S. 1992. Webspinners of Panama (Embiidina) (pp. 122-141). In: QUINTERO, D. & AIELLO, A. (eds). *Insects of Panama and Mesoamerica*. OUP, Oxford, New York, Tokyo. xxii, + 692 pp.
- ROSS, E. 2009. World List of Extant and Fossil Embiidina. Available online at http://researcharchive.calacademy.org/research/entomology/Entomology_Resources/embiilist/index.htm [consulted 19/8/2012].
- SAUSSURE, H. de 1896a. Two Embidae from Trinidad. *Journal of the Trinidad Field Naturalist Club* 2: 293-294.
- SAUSSURE, H. de 1896b. Note sur la Tribu des Embiens. *Mitteilungen der schweizerischen entomologische Gesellschaft* 9: 339-355.

Cicadas in Switzerland: a scientific overview of the historic and current knowledge of a popular taxon (Hemiptera: Cicadidae)

Thomas HERTACH & Peter NAGEL, University of Basel,
Department of Environmental Sciences, Biogeography
St. Johannis-Vorstadt 10, CH - 4056 Basel, Switzerland.
thomas.hertach@unibas.ch

Cicadas in Switzerland: a scientific overview of the historic and current knowledge of a popular taxon (Hemiptera: Cicadidae). - Cicadas are charismatic and are widely appreciated, even by the general public, but knowledge of species diversity and distribution is patchy, incomplete and sometimes misleading. This study presents an overview on the historic and current knowledge on the cicadas of Switzerland. For the first time, data retrieved from historic and recent literature, review of public and private collections and detailed recent field-work including up-to-date recording techniques have been combined. Our work during the last decade has resulted in the doubling of the number of known species. We now report the existence of ten native species in Switzerland: *Cicada orni*, *Lyristes plebejus*, *Tibicina quadrisignata*, *T. steveni*, *T. haematodes*, *Cicadetta montana* s. str., *C. cantilatrix*, *C. sp. aff. cerdaniensis*, *C. brevipennis* and *Tettigettna argentata*. All species are presented, with detailed distribution maps, data on habitat and conservation status. Centres of cicada diversity are the southern Swiss cantons of Valais, Ticino and Geneva. Nine species have restricted habitat requirements, seven species are rare and three species are of high national conservation importance in Switzerland.

Keywords: distribution - habitat requirements - threat - *Tibicina* - *Cicadetta montana* species complex - flagship species - erroneous records - Tibicininae - Cicadinae.

INTRODUCTION

Cicadas (Cicadidae) form an attractive group of potential flagship species that are recognized and liked by many non-scientists in Switzerland. Some Swiss species attract attention by their loud calling songs, but many species are rare and very difficult to see or capture. Furthermore, recent studies have shown Central European cicadas to be taxonomically interesting. Acoustic investigations have demonstrated that *Cicadetta montana* s. l. consists of several species with clearly different calling song patterns (e.g. Gogala & Trilar, 2004; Sueur & Puissant, 2007a). The consideration of song patterns as species-specific characters has permitted a reassessment of the Swiss cicada fauna (Hertach, 2004, 2007, 2011).

Very few publications are available on Swiss cicadas, although the country includes Mediterranean regions in Ticino and Grisons and a xerothermic valleys in the Valais that potentially favours high diversity in cicadas. Before 2004, only four references in scientific journals referred to Swiss cicadas in their titles (Artmann, 1987; Pillet, 1993; Vernier, 1996; Sueur *et al.*, 2003). In contrast more than twenty publications on local occurrences of *Cicadetta montana* s. l. (e.g. Hübner, 1904; Schwoerbel, 1957; Müller, 1969; Eitschberger, 1972; Niehuis & Simon, 1994; Dorda, 2012; Meineke, 2012) and *Tibicina haematodes* (e.g. Geisenheyner, 1887; Vogel, 1935, 1937; Schwoerbel, 1957; Niehuis & Simon, 1994) in Germany have been published, even though the cicada fauna of Germany is less rich (Nickel & Remane, 2003; Biedermann & Niedringhaus, 2004; Kung *et al.*, 2001; Meineke, 2012).

The poor understanding of Swiss cicada distribution and diversity is a big hurdle to plan and implement conservation strategies for their protection. A summary of our basic knowledge of this group has been lacking completely for Switzerland. Our work intends to update the knowledge on the species diversity, distribution, and habitat and conservation requirements of cicadas in Switzerland. The presented data are based on field studies conducted during the last decade, studies of entomological collections and published data from the 18th century onwards.

MATERIAL AND METHODS

Over the last years systematic field work has been conducted in regional projects across the country: eastern part of the Jura Mountains (Cantons of Aargau, Solothurn, Basel-Stadt and Basel-Land), Canton of Ticino, Canton of Graubünden (Grisons), Lake Geneva Basin (Canton of Geneva and parts of Canton of Vaud). Other regions have been visited occasionally. Regions and subregions mentioned several times within this work are illustrated in Fig. 1.

For recent records, the presence of a species at a locality was normally detected acoustically. Recordings were made with a Marantz PMD 660 (sampling frequency at 48 kHz) and mainly analysed using Raven Pro 1.3 (Cornell Lab of Ornithology). The number of singing individuals was counted or estimated. For detecting and recording the species in the *Cicadetta montana* complex, which sing in a high frequency range (10 - 18 kHz), an ultrasonic detector (Petterson D 200) was used whose microphone was fitted into a Telinga parabola or a smaller parabola with a 15 cm diameter (adapted from Popov *et al.*, 1997).

Records of cicadas from the public collections of the Swiss natural history museums (Aarau, Basel, Bern, Chur, Frauenfeld, Fribourg, Geneva, Lausanne, Liestal, Lucerne, Lugano, Neuchâtel, Olten, Schaffhausen, Sion, Solothurn, St. Gallen, Winterthur), of the Swiss Federal Institute of Technology Zurich and of the Agroscope Changins Nyon have been reviewed and records compiled. A few museums outside Switzerland (Paris, Vienna, Ljubljana) and private collections (Pillet, Marchesi, Chittaro, Vernier, Keim, Artmann) have been checked for usable data. We attempted to review all potentially relevant regional, national and international zoological journals or series for references on cicadas from Switzerland, with particular attention to local publications for the Cantons of Ticino, Valais, Grisons, Vaud and Geneva. Digital literature databases have been searched using relevant key words. The data from the



FIG. 1

Regions (capital letters) and subregions (normal letters) used for cicada recording within this study.

Swiss Central Fauna Data Bank was included (CSCF, Neuchâtel). Unexpected or questionable records from all these sources have been verified by personal contacts with other entomologists or naturalists where possible. Several requests have been published in newspapers and magazines to stimulate reports on observations of the few remarkable species in the Basel region, Ticino and the Lake of Geneva Basin.

According to the Swiss graticule, chorological data is visualized in a grid of 5 km x 5 km cells with ArcGIS (map source: <http://srtm.csi.cgiar.org> and <http://www.diva-gis.org>). Distribution maps are based on the two parameters “abundance” and “time period of the observation” each of them divided into three categories (Table 1). Note that “time period” is the latest record and “abundance” is the highest density and these are presented in the maps for each cell. Observations made within one time period but from different locations are pooled for each cell. Although we only include reliable records, the level of certainty is different when comparing literature references, voucher specimens or data gathered during field-work. For example, voucher specimens are not helpful in distinguishing species morphologically in the *Cicadetta montana* complex. Only verified acoustic records can be included. In contrast, acoustic field observations of some species belonging to the genus *Tibicina* Amyot, 1847 are uncertain, because the songs are very similar (Sueur & Aubin, 2003). Within this genus we have normally integrated records based on either voucher specimens or digital recordings of the calling song analysed on the computer. The distribution maps show some unpublished records from adjoining countries of Switzerland that could be helpful for the understanding of the chorological pattern.

Based on historical data, the current distribution and habitat requirements, the level of extinction threat of the species is estimated for Switzerland. These data will provide information for Red List assessment of each species. Furthermore, we discuss the abundance of species found in Switzerland in an international context. We highlight those important populations that occur within the borders of Switzerland and are therefore of high national conservation importance for the country.

Nomenclature follows Puissant (2006), Gogala (2012, www.cicadasongs.eu) for European species, Boulard (1981), Hayashi & Saisho (2011) for exotic taxa and Moulds (2005) for higher classification. We provide German common names in addition to previous works. We have chosen the most established and accurate term in cases with several common names.

ACRONYMS

Museums (cf. <http://hbs.bishopmuseum.org/codens/codens-inst.html>)

BNM	Bündner Naturmuseum Chur
ETHZ	Eidgenössische Technische Hochschule Zürich (Swiss Federal Institute of Technology)
MCSN	Museo Cantonale di Storia Naturale Lugano
MHNG	Muséum d'Histoire Naturelle de la Ville de Genève (Geneva)
MHNN	Muséum d'Histoire Naturelle Neuchâtel
MNHN	Muséum National d'Histoire Naturelle Paris
MZLS	Musée de Zoologie Lausanne

NAAG	Naturama Aarau
NHMB	Naturhistorisches Museum Basel
NMBE	Naturhistorisches Museum der Burgergemeinde Bern
NMLS	Natur-Museum Luzern (Lucerne)
NMS	Naturmuseum Solothurn
NMT	Naturmuseum Thurgau Frauenfeld
NMWI	Naturmuseum Winterthur

Swiss Cantons

AG	Canton of Aargau
BE	Canton of Bern
BL	Canton of Basel-Land
FR	Canton of Fribourg
GE	Canton of Geneva
GR	Canton of Graubünden (Grisons)
LU	Canton of Lucerne
TG	Canton of Thurgau
TI	Canton of Ticino
UR	Canton of Uri
VD	Canton of Vaud
VS	Canton of the Valais
ZH	Canton of Zurich

TABLE 1. Parameters and their categories for the production of the distribution maps.

Parameter	Category	Description
Abundance	High	more than 30 specimens in <i>Cicadetta</i> , <i>Tettigettalna</i> and <i>Cicada</i> , more than 20 specimens in <i>Lyristes</i> and <i>Tibicina</i>
	Low	less than 30 specimens in <i>Cicadetta</i> , <i>Tettigettalna</i> and <i>Cicada</i> , less than 20 specimens in <i>Lyristes</i> and <i>Tibicina</i> , but reproductive population expected or confirmed
	Single specimen	only one specimen reported within one time period, reproductive population not expected
Time period	2000-2011	recent observations
	1950-1999	elderly observations
	before 1950	historic occurrences
Data source	Field observation	observations unpublished, stored in the Swiss Central Fauna Data Bank or/and made by the authors (discrimination normally according to acoustic characters)
	Collection	specimens found in public and private collections (discrimination according to morphology)
	Literature	references published by other scientists or naturalists

RESULTS

GENERAL OVERVIEW

1288 field records from Switzerland have been included in the final analysis, most of them gathered within the last 10 years and 824 made by the first author. The

study is supported by 128 sufficiently labelled voucher specimens from public and private collections and by 194 reliable and spatially precise literature references, 78 % referring to Pillet (1993) (Table 2). Literature references have been found in general works on insects, descriptions of Swiss nature and the popular science literature, rather than in specific scientific entomological publications.

Moffet *et al.* (1634) looked intensively for cicadas in "Helvetia" but without any success, although it is not clear if they visited Ticino and the Valais. They were convinced that other contemporary naturalists had confused cicadas with grasshoppers and other insects. In the 18th and early 19th century a general confusion existed in the taxonomy and nomenclature of European cicadas. Even common and currently well-known species have been mixed up due to inexact descriptions or illustrations, missing type specimens and scarce chorological data. For example, Dietrich (1872) was, according to our knowledge, the first Swiss author to use the name *Cicadetta montana* (Scopoli, 1772), exactly one century after the description. Previously this species was erroneously called *Tibicina haematodes*, *Cicada orni* or *Cicadetta concinna* by different authors (e.g. Sulzer, 1761; Fuesslin, 1775; Heer & Blumer, 1846; Bremi, 1849). These confusions sometimes lead to difficulties in the interpretation of historical data.

Fuesslin (1775, p. 24) mentions the four cicadas "*Cicada orni*", "*Cicada plebeja*", "*Cicada haematodes*, der Blutring" and "*Cicada violacea*, die Blaue" in his list of Swiss insects. "*Cicada orni*" and "*Cicada plebeja*" are obviously identical to the species currently known as *Cicada orni* Linnaeus, 1758 and *Lyristes plebejus* (Scopoli, 1763). "*Cicada haematodes*" is referenced to Sulzer's illustration (1761, plate 10, fig. 65) which, however, shows *Cicadetta montana* s. l. (see e.g. Hagen, 1856b; Fieber, 1876). The fourth species, "*Cicada violacea*", remains mysterious (see section "Comments on other species" below). Sulzer (1761) and Von Salis (1807) did not mention any cicada records from Switzerland.

Bremi (1849) recorded five cicada species from Switzerland, but with the exception of "*Cicada concinna*" which can reliably be referred to *C. montana* s. l., does not name the remaining four species. Some species must have been locally abundant in the Valais and Ticino, as Bremi stated (1849, p. 333) "für feine Ohren in belästigender Menge" (= in irritating density for sensitive ears). Hagen (1855, 1856a, 1856b) refers to the local knowledge of Bremi. The information on Swiss cicadas that these early studies contributed was substantially greater than was to be published in the next hundred years.

Stoll (1901) listed the three species *Cicada orni*, *Tibicina haematodes* (Valais) and *Cicadetta montana*. Robert (1937) knew five species sporadically entering Central Europe, but only provides one record for a more precisely defined area (*C. montana* s. l.). Other authors mentioned cicadas casually and only generally as remarkable representatives of the insects (e.g. Stabile & Stabile, 1856; Bettelini, 1919; Zschokke, 1928; Segantini, 1937), completely omit this group despite promising general study titles (e.g. Pavesi, 1873; Carlini, 1887), or do not provide any information for Switzerland (Melichar, 1896; Oshanin, 1912). Nast (1972) listed seven species in his catalogue on Palaearctic Auchenorrhyncha for Switzerland, but three of them are obviously erroneous as will be demonstrated below. The author corrected some of them himself when listing only five species in his second catalogue (Nast, 1987).

TABLE 2. Number of records per species integrated to the maps: field records, literature references and voucher specimens and grid cells occupied (without records from the neighboured foreign countries).

	Field*	Literature	Vouchers	total	Grid cells
<i>Cicada orni</i>	309	98	57	464	68
<i>Lyristes plebejus</i>	65	8	15	88	15
<i>Tibicina quadrisignata</i>	35	47	27	109	18
<i>Tibicina steveni</i>	26	36	21	83	16
<i>Tibicina haematodes</i>	5	0	10	15	3
<i>Cicadetta montana</i>	532	1	0	533	182
<i>Cicadetta cantilatrix</i>	233	4	0	237	66
<i>Cicadetta</i> sp. aff. <i>cerdaniensis</i>	39	0	0	39	11
<i>Cicadetta brevipennis</i>	31	0	0	31	8
<i>Tettigettalna argentata</i>	13	0	0	13	2
total	1288	194	128	1610	

* Field records which have already been published in own studies and vouchers in the own private collection are only counted in this second column.

The absence of publications on the cicadas from the southern part of the Alps (Ticino and some valleys in Grisons) is particularly notable. Neither the first 99 volumes of the *Bollettino della Società ticinese di scienze naturali* nor the 300 issues of the more popular *Il nostro paese* include a single reference to cicadas at the local or national scale. In contrast many non-scientists from these regions perceive and know well the song of „le cicale“, which normally refers to *Cicada orni*. Perty (1879, p. 315) writes about two species occurring in Ticino, one singing by day and one by night, but the latter observation must refer to an Orthoptera species. A detailed study of the cicadas of Ticino has just been published (Hertach & Pollini Paltrinieri, 2012).

Cicadas have been treated in popular, well illustrated literature on nature in the Valais (Bille, 1980; Bille & Werner, 1986; Delarze, 1988; Oggier, 1995). Pillet (1993) published the first modern and comprehensive work on cicadas focussing on the Valais region. He reported five species, each of them presented with detailed distribution maps and ecological data: *Cicada orni*, *Lyristes plebejus*, *Cicadetta montana* (Scopoli, 1772), *Tibicina quadrisignata* (Hagen, 1855) and *T. haematodes* (Scopoli, 1763). He concludes that these five species are the only ones in Switzerland. Cicadas from the Valais have been observed by different local naturalists since the study by Pillet, with some notable records published in the annual reports of the *Bulletin de la Murithienne* (Sierro & Keim, 1999; Sierro *et al.*, 2000; Marchesi *et al.*, 2002).

In more recent literature on a national scale, Günthart & Mühlethaler (2002) and Holzinger *et al.* (2003) listed the six species *C. orni*, *L. plebejus*, *T. quadrisignata*, *T. haematodes*, *C. montana* and *Cicadatra atra* (Olivier, 1790) mainly referring to Schedl (2000). Almost the same species spectrum is available from the Fauna Europaea project, solely missing *T. quadrisignata* (Hoch, 2011). In 2007, the small cicada *Tettigettalna argentata* (Olivier, 1790) was found for the first time in Switzerland (Hertach, 2008). Additionally, the presence of *Cicada orni* and *Lyristes plebejus* has been confirmed within the current study, besides the genera *Cicadetta* and *Tibicina* which have to be discussed in more detail.

CICADETTA MONTANA SPECIES COMPLEX

In the 18th and 19th centuries many species and subspecies similar to *Cicadetta montana* (Scopoli, 1772) were described using morphological characters. Most authors later assigned them to the two taxa, *C. montana* and *C. concinna* (Germar, 1821 = *C. podolica* Eichwald, 1830) for Central Europe, since the characters showed large and overlapping variability (e.g. Duffels & Van der Laan, 1985; Nast, 1987; Schedl, 2000). The introduction of acoustic methods has revealed sibling species even in Central Europe, which is probably one of the most astonishing taxonomic findings in entomology for this region in recent decades (Gogala & Trilar, 2004; Puissant & Boulard, 2000; Sueur & Puissant, 2007a). Currently, twelve European species, most of them from Greece, have been described within the complex (Gogala *et al.*, 2011; Hertach, 2011).

Acoustic differences among cicada species have been noted earlier and it would not do justice to the 19th century's entomologists from Germany and Switzerland to assume they did not consider discriminating species on this basis. Bremi (1849, p. 333) wrote 150 years before the elucidation of the *Cicadetta montana* species complex: "Ich vermthe, dass sich neben jener gewöhnlichen Art noch eine oder zwei in unsern warmgelegenen Laubwäldern vorfinden. Sie zu entdecken, wird man auf den Gesang derselben lauschen müssen, der unter den Arten sehr verschieden ist, wie Hr. Professor Von Siebold an zwei bei Freiburg im Breisgau entdeckten Arten beobachtet hat." [= I suppose that one or two species will be detected in our thermophilous deciduous forests in addition to the common species. You have to listen to their songs which are clearly different between species, what has been observed by Professor Von Siebold in two detected species near Freiburg (Germany)]. It seems that Siebold (1847, p. 10) had still misinterpreted the songs in his own work two years before. He described a song that repeated echemes 10 to 12 times in a fast rate. This description fits well to the song of *Cicadetta cantilatrix* Sueur & Puissant, 2007a. And he concluded: „... geben ... ziemlich laute Töne von sich, welche, wenn diese Sänger in grossen Gesellschaften auf Bäumen und Buschwerk umher vertheilt ihre Stimme hören lassen, so in einander schmelzen, dass nur noch ein einziger ununterbrochener Ton durch die Luft getragen wird“ (non-literal translation: If calling males occur in dense populations, the tones will merge resulting in one single steady sound). In fact, Siebold probably observed a syntopic population of *Cicadetta cantilatrix* and *C. montana* s. str. whose song fits well with the steady song pattern. Neither Bremi nor Siebold published later descriptions of a new species and their findings were not commented on by subsequent authors.

Artmann (1987) described the song of *C. cantilatrix* from the Swiss Jura Mountains in words, but he concluded to have found a regional dialect of *C. montana* s. str. It took another 15 years until these acoustic differences were investigated more deeply (Puissant & Boulard, 2000; Gogala & Trilar, 2004; Hertach, 2004). Currently we know that in Switzerland four sibling species of the complex exist (Hertach, 2007, 2011).

GENUS *TIBICINA* AMYOT, 1847

The genus *Tibicina* consists of larger sized species (up to 85 mm wingspan), singing loudly and with fairly similar continuous song patterns. The species can be

separated relatively easily by the specific coloration of the thorax and the wing venation, but are difficult to catch as solitary singers. Bugnion (1890) listed “*Cicada haematodes*” and “*Cicada viridinervis*” for the Valais, the latter currently known as a variety of *Tibicina haematodes* described by Fieber (1876). Bugnion had already realized that two different taxa occur in the Valais. Other authors solely mention *Tibicina haematodes*, the most widely distributed European species, as the single Swiss species of this genus occurring in the Valais (Meyer-Dür, 1860; Stoll, 1901; Kuntze, 1931). Pillet (1993) was the first to publish that *Tibicina quadrisignata* occurs in the Valais. Ten years later, Sueur *et al.* (2003) published that the second species is the eastern species *Tibicina steveni* (Krynicky, 1837) and that *T. haematodes* does not occur in the Valais. The surprising presence of *T. steveni* in the Valais had actually been reported indirectly long previously. Hagen (1855) assigned a specimen received from Bremi to his variety “*Cicada sanguinea*” which he supposed to be identical to Krynicky’s “*C. steveni*”. He also wrote that none of the Swiss specimens belonged to *T. haematodes*.

Nevertheless, a single reference by Vernier (1996) indicated that *T. haematodes* could belong to the Swiss fauna. He listed voucher specimens deposited in the MHNG (see also Hollier, 2012). They were collected in the Canton of Geneva in the first half of the 20th century. We studied these vouchers and confirm Vernier’s comment. *T. haematodes* is, therefore, the tenth, but extremely rare indigenous Swiss species, the third of the genus *Tibicina* (Fig. 2).

ANNOTATED LIST OF SWISS CICADAS

Cicada orni Linnaeus, 1758

German common name: Mannazikade (e.g. Remane & Wachmann, 1993; Schedl, 2000)

French common name: La Cigale de l’orne (Pillet, 1993)

DISTRIBUTION (Fig. 3)

Cicada orni is the most popular European cicada due to its remarkable chorus song and its wide distribution area. If Swiss non-scientists speak about cicadas they normally refer to this species.

Fuesslin (1775) knew *C. orni* from the Valais as “very abundant”. Saussure (1780) wrote that *C. orni* is completely missing in the Geneva region and provides herewith an interesting absence record in very old literature. Labram & Imhoff (1845) reported it from the most southern parts of Switzerland where it was locally abundant. Curti (1846) thought *C. orni* to be restricted to Ticino, some parts of Grisons and found occasionally in the Valais. Seiler (1847) listed the species as uncommon for the Canton of Schaffhausen, but we doubt its validity since he does not report *Cicadetta montana* s. l. Hagen (1856a) cites Bremi who has found it as the most common species in Ticino. Tschudi (1872) listed *Cicada orni* as abundant in both Ticino and Valais with a record altitude of “3800 feet” (≈ 1150 m a.s.l.) for the upper Valais. Rougemont (1880, p. 33) mentioned “un charivari vraiment méridional” at Fully (VS) (= a true Mediterranean pandemonium). Bugnion (1890) described the species as very common from Martigny (VS) to Sierre (VS), but missing at Montreux (VD) and Lausanne (VD). Stoll (1901) repeated the occurrence in the Valais and Ticino and added a remarkable observation



FIG. 2

Three species of the genus *Tibicina* deposited in Swiss Museum collections: *T. quadrisignata* (♂ on the top, Valais, 1928, leg. Cerutti, MZLS), *T. steveni* [♀ in the middle, Sierre (VS), leg. Maerky, MHNG] and *T. haematodes* [♂ below, "Pt. Butin" (GE), 1943, leg. Schauenberg, MHNG]. Bar = 1 cm.

by Dr. Ris on a Manna Ash (*Fraxinus ornus*) from the city of Zurich ("Kantonschule"), which seems reliable. Another two records far away from the known range have been published from Mont Vully (FR) (Musée d'histoire naturelle Fribourg, 2004) registered in the 1960's (Beaud, pers. comm.) and from Vevey (VD) (1976;

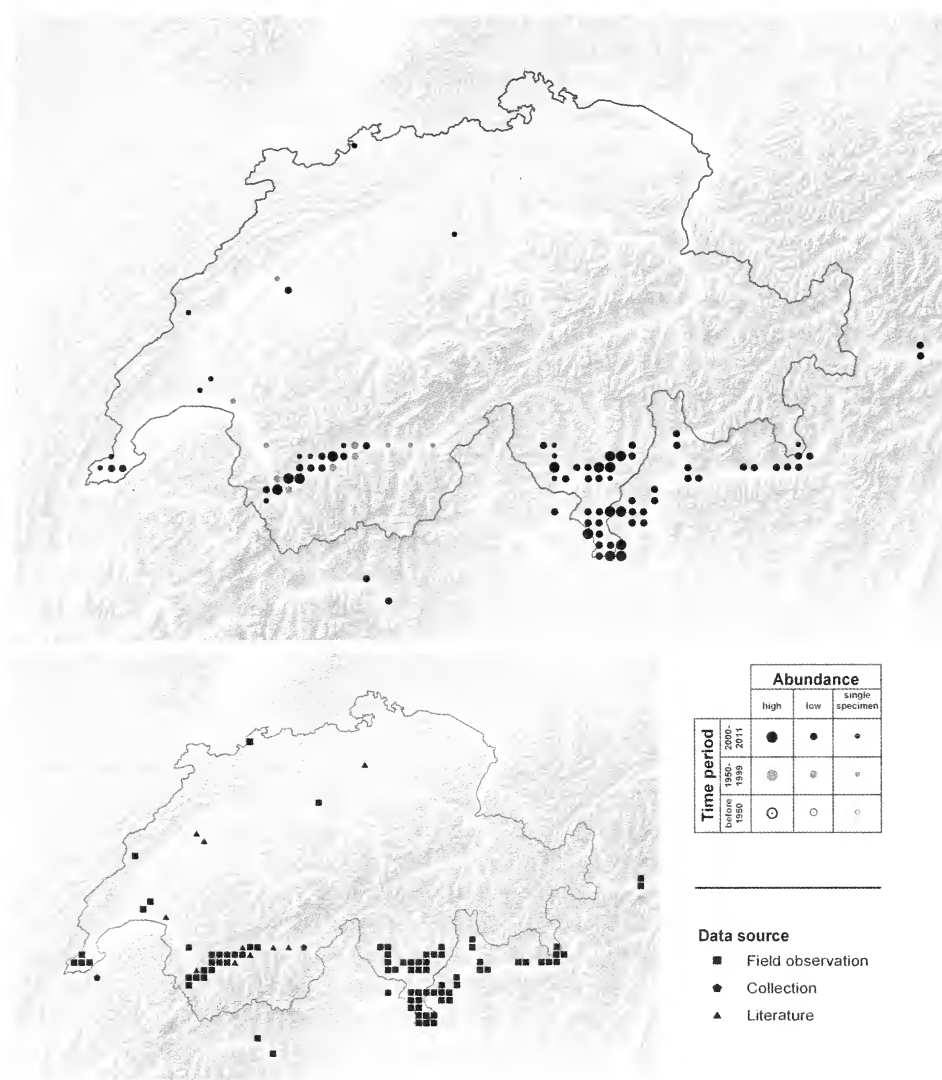


FIG. 3

Distribution map of *Cicada orni* (top) including the data source for the records presented (below).

Barbey, 2010). Bille (1982) probably refers to *C. orni* when writing that the fabulous concert can sporadically be heard in the Lake Geneva Basin and at the southern base of the Jura Mountains. Many of the older records are not clearly localized but are normally overlapping with regions with many recent observations. The distribution map for the Valais provided by Pillet (1993) is very detailed and even presents two abundance classes. Among 104 sufficiently labelled specimens identified in collections during the present study, 90 originate from the Valais, 8 from the Mesocco Valley (GR)

and only 6 from Ticino. Eight of them are remarkable with respect to the current distribution: Grono (GR) (1883, four specimens, NHMB), Roveredo (GR) (1922, NHMB), Brig (VS) (1929 and 1980, NHMB), Valle Morobbia (TI) (1937, ETHZ). We consider a voucher labelled solely "Aarau" (AG, NAAG) doubtful.

The current distribution area is well known and almost congruent with the historical data. *C. orni* populations are restricted to the lower Valais from Martigny to Sierre, the most southern parts of Ticino (South of Lugano) and to a belt extending from the lowest Centovalli (TI) along the northern slope of the Piano di Magadino (TI) to the Mesocco Valley (GR). The species is locally common.

Local observers indicate for example for Grono and Roveredo (Mesocco Valley) that the species has appeared only the last few years. According to voucher specimens collected at the end of the 19th and at the beginning of the 20th centuries, it is therefore more accurate to speak about a supposedly re-colonisation.

Similar to older observations, isolated singers sporadically appear outside the continuous distribution area as far as south-western Germany (Nickel, 2003), often in urban areas and gain remarkable publicity: Murten (FR) (25.6.2003; Musée d'histoire naturelle Fribourg, 2004), Lausanne (VD) (13. and 19.7.2010; Ducret, 2010 and Bertaudon/Barros, pers. comm.), Epalinges (VD) (July 2010; Alexander, pers. comm.), Binningen (BL) (2.8.2010; Blattner, pers. comm.), Sursee (LU) (9.7.2011; Birrer, pers. comm.) and Ste-Croix above Yverdon (VD) (August 2011; Burnier, pers. comm.). In the Geneva agglomeration, the records have accumulated in a manner that suggests the establishment of a small new population (see also Hollier, 2012). We assembled eleven reliable observations between 2003 and 2011 in this region, eight communicated by naturalists (Prosenc, Hollier, Dandliker, pers. comm.), two printed in newspapers (Grosjean, 2008; Nikolic, 2010) and one even broadcasted on national television (Radio Télévision Suisse Romande, 2010). Some of these isolated singers have probably been transported as larvae in the root balls of plants, as is the case for the Murten (FR) specimens, which were introduced with olive trees for an exhibition. Others have reached their singing site on their own, which probably applies to all observations in the Lake of Geneva Basin.

Populations are normally restricted to altitudes below 600 m a.s.l. in Ticino and Grisons and 800 m in the Valais, but solitary singers can exceptionally rise up to 1530 m a.s.l. (La Forclaz, VS; Marchesi, pers. comm.).

ECOLOGY AND THREAT

Cicada orni is the most eurytopic species of the Swiss cicadas, colonizing man-made habitats such as vineyards along forest edges, woods, hedges and solitary trees and even parks and gardens in urban areas. Nevertheless, some of the most important populations are found in natural habitats of generally high conservation value such as forests dominated by Downy (*Quercus pubescens*) and Sessile Oak (*Quercus petraea*) (= *Quercion pubescenti-petraeae*, see Delarze & Gonseth, 2008) for the Valais and a plant association characterized by Downy Oak, Turkey Oak (*Quercus cerris*), Hop Hornbeam (*Ostrya carpinifolia*) and Manna Ash (*Fraxinus ornus*) for Ticino (= *Orno-Ostryon*, see Delarze & Gonseth, 2008). A long exposure to the sun is very important for this species, therefore most habitats have south-facing slopes. The distribution area is limited by the less favourable climate in other parts of Switzerland.

Given its habitat associations we assume that *C. orni* will extend its distribution area if a predicted rise in temperatures will occur. Currently this can probably be observed in the Lake Geneva Basin, where the species obviously did not occur in the 18th and 19th century (Saussure, 1780; Bugnion, 1890). The species is not endangered but we consider it to be important for public awareness and education with respect to bioacoustic experience and climate change.

***Lyristes plebejus* (Scopoli, 1763)**

German common name: Grosse Zikade (Gogala, 2002)

French common name: La grande Cigale commune (e.g. Boulard, 1995)

DISTRIBUTION (Fig. 4)

Lyristes plebejus is the second largest European cicada after the South-Eastern European species *Lyristes gemellus* Boulard, 1988, and has a very loud and distinctive song pattern. The great Swiss savant Albrecht Von Haller (1765, p. 77) knew “die echte Cicade der Alten” (= the true cicada of the ancients) from Aigle (Chablais, VD) that we assume probably refers to *Lyristes plebejus*. This is the first record found for cicadas in Switzerland. Fuesslin (1775) reports the species from the so-called “Italienische Vogteien” (= Italian Bailiwicks; at that period comprising the Swiss Ticino as well as the Italian Valtelline Valley and Chiavenna region) and from Roche (Chablais, VD). Schnetzler (1877) mentioned *L. plebejus* from Bex (VD) one century later, located like Roche in the neighbourhood of Aigle. Pillet (1993) concluded that the remarkable species must have been quite frequent in the Valais in the 19th century referring to a notice and several specimens found in the MHNG. Milde (1866), Huber (1916) and later Schedl (2000) mentioned the species only for the most southern parts. Nevertheless, concrete historic records from Ticino are missing in the literature and in the museum collections. Vernier (1996) could not find *L. plebejus* in Ticino, in contrast to the local abundant *C. orni* during his journey in summer 1994. Schertenleib observed the species several times at Lake Neuchâtel during the first half of the 20th century (Vernier, 1996). We could not prove this historic occurrence, and with the recent death of Schertenleib and without information from his colleagues, the Lake Neuchâtel records remain uncertain. Vernier also mentioned a nymphal skin from the Canton of Geneva found in the same period (1945) and preserved in the MHNG, but this exuvia belongs to the genus *Tibicina* (T.H. vidit 2010). Pillet (1993) observed the species only three times for the Valais between 1985 and 1993. Scherdlin (1910), Döderlein (1913) and Huber (1916) also reported few records from the French Alsace region which seem to be reliable.

Lyristes plebejus is currently a very rare species in Switzerland and with an unusual distribution pattern. It is mainly restricted to two established, dense populations situated in the Lugano region (TI). The first includes the slope between Bré – Gandria – Castagnola, the second located in the San Salvatore Mountain, both with a maximum of 25 calling males. The two populations are described for the first time within this study. A third, new population seems to be established in the surrounding of Verchiez (Chablais, VD). Keim (pers. comm.) registered between two and eight singing specimens in the years 2004, 2005, 2007, 2009 and 2010. Our survey of this site revealed the presence of 10 to 12 males in 2012, but no other specimens in the

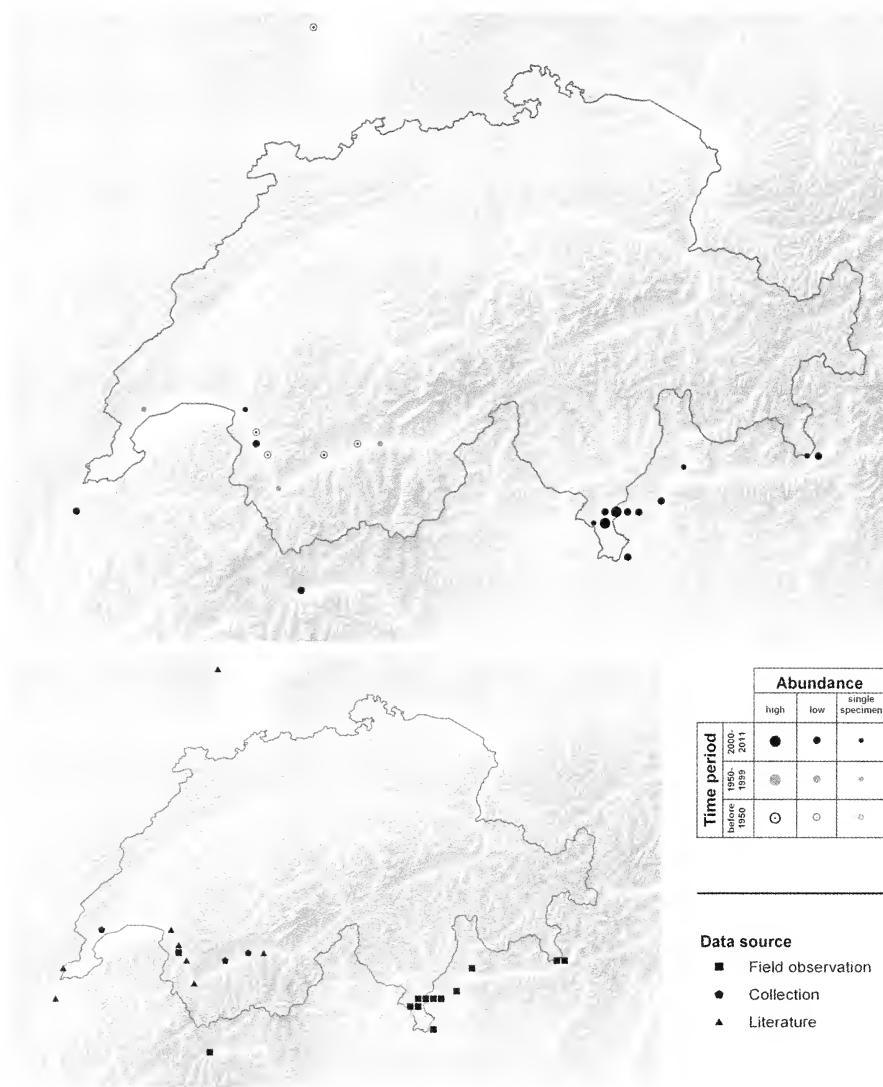


FIG. 4

Distribution map of *Lyristes plebejus* (top) including the data source for the records presented (below).

whole region. Interestingly, Verchiez is situated in the municipality of Aigle, where Von Haller (1765) had indicated the species 250 years before.

The species can sporadically be found far away from established populations with isolated singers especially in the Lake Geneva Basin. Vernier (1996) discussed in detail one record from the Vallon d'Allondon (Russin, GE) in 1995. Further observations have been made in 1999 in Gland (VD) (♀ drowned in a pool, leg. Breitenmoser), in 2004 at La Tour-de-Peilz (VD) (det. Martin/Göldin; Muhieddine,

2004), and potentially even in Allschwil (BL) in 2006 (Currat, pers. comm.). Established populations can be found less than two kilometres behind the Swiss border near the Poschiavo Valley (GR) in the Valtellina (Italy). Juillerat (pers. comm.) heard one specimen singing at the Swiss side of the border in 2009 (Campocologno). *L. plebejus* is also currently known from the Val des Usses in Haute-Savoie (France; Vernier, 1996 and Bal, pers. comm.).

ECOLOGY AND THREAT

The two habitats in Ticino consist of almost natural, rocky and steep slopes (*Orno-Ostryon*, see previous chapter). Here, at the northern limit of its range, *L. plebejus* is restricted to this mostly undisturbed, Mediterranean landscape, while in its core area some populations even colonize city parks. In spite of the rareness, the species does not seem to be threatened in Ticino by habitat loss. The habitats are scarcely influenced by human activities and classified as protected “dry habitats of national importance” by Swiss authorities.

In contrast, *L. plebejus* has become extinct in the Valais (Keim, 1999). Pillet (1993) could not find a cogent reason for the dramatic decline. The population in the Chablais is restricted to the close surrounding of three cliffs with sparse forests dominated by oaks (*Quercus* sp.). This site is almost natural as in Ticino but in vicinity of intensively cultivated vineyards. The recent observations may indicate a re-colonisation in the south-western part of Switzerland which could be promoted by climate change. The Chablais (VD) could play an important role for this species with its steep rocky slopes and the mild climate.

Tibicina quadrisignata (Hagen, 1855)

German common name: Schwarzer Scherenschleifer

French common name: La Cigale quadrisignée (e.g. Pillet, 1993)

We could not find a common German name for this species. “Scheereschliffer” (= scissor grinder) is an old popular and local name used for *T. haematodes* from southern Germany (Geisenheyner, 1887; Jacobs & Renner, 1988) and representing the sound of all species of the genus in a suitable and inventive manner. The black coloration of the wing venation is diagnostic within the genus for Central European species.

DISTRIBUTION (Fig. 5)

Tibicina quadrisignata is distributed in the western Mediterranean region and has been confirmed recently for the Mediterranean regions of France (Puissant, 2006) and for Portugal (Sueur *et al.*, 2004). The species is also reported from the Aosta Valley in Italy (Schedl, 2000 and pers. data). Pillet (1993) was the first to report this species for Switzerland and presented a detailed distribution map with occurrences in the upper Rhone Valley (VS) from Grenchiols to Salgesch and in parts of the very dry Visp Valleys. He concludes a strict vicariance with *T. haematodes* (later corrected to *T. steveni*), the latter colonizing the lower, western parts of the Rhone Valley and some side valleys west of Salgesch, including the Finges Forest (VS, Sierre region).

One voucher specimen (1977, NMWI) and our acoustic recordings suggest that the Finges forest population belongs to *T. quadrisignata*, five further specimens are

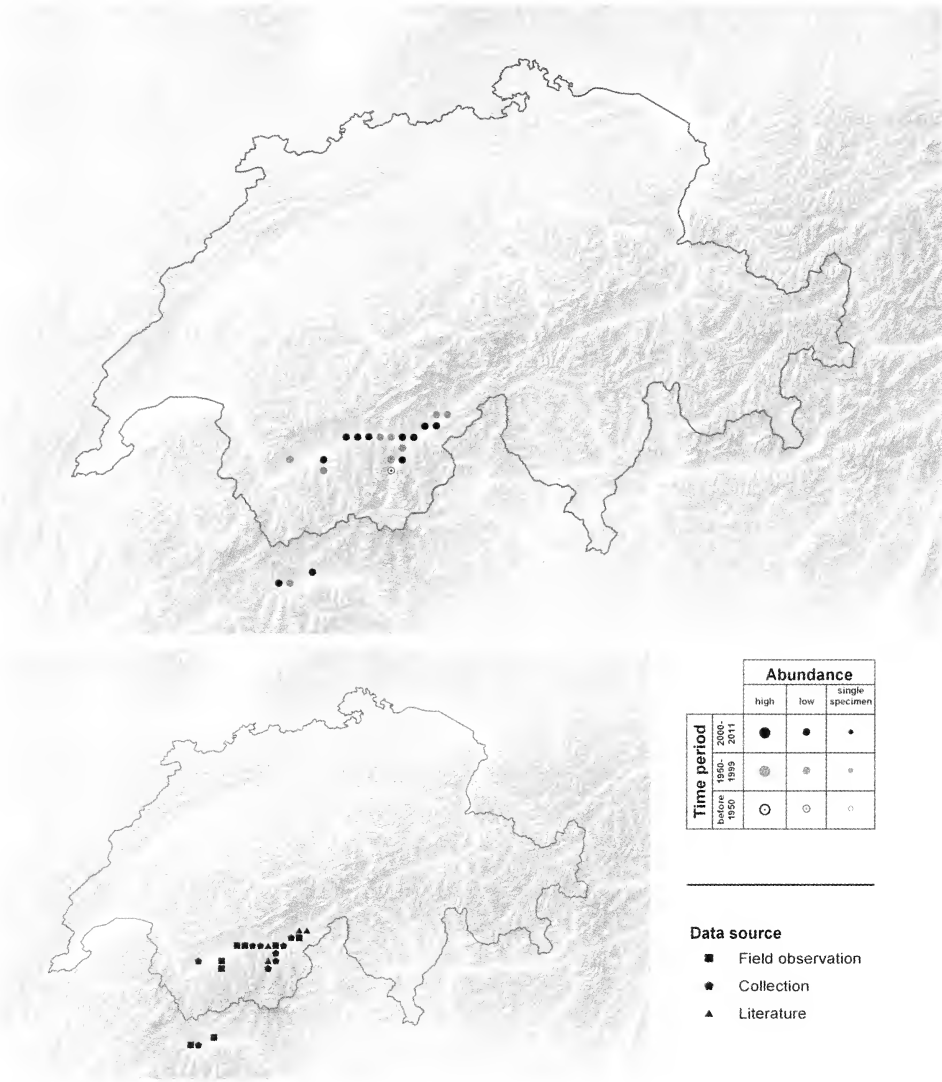


FIG. 5

Distribution map of *Tibicina quadrisignata* (top) including the data source for the records presented (below).

labelled with “Sierre” (NMHN and MNHG). The limit of the known distribution range is therefore slightly shifted westward for *T. quadrisignata* when comparing to Pillet (1993). Moreover the allopatry seems not to be that strict. *T. quadrisignata* has also been found clearly west of Sierre but only very few observations can be validated: Chamoson (Sierro & Keim, 1999; 2 ♂ leg. Carron, MHNN and private collections of Keim), Bramois [Sierro *et al.*, 2000; ♀ seen (Keim, pers. comm.)] and Euseigne (Praz, pers. comm.). Vernier (pers. comm.) knows one site where *T. quadrisignata* and *T. ste-*

veni occur in complete syntopy in the Val d'Hérens. This range overlap makes the delimitation of the distribution areas of *T. quadrisignata* and *T. steveni* more complicated. The songs are very difficult to discriminate in the field and it is probable that Pillet was not able to verify all of his observations, neither by analysing fine song differences on computer (Sueur & Aubin, 2003) nor by checking coloration characters. There is no evidence that *T. steveni* occurs to the east of Sierre, and all other 19 voucher specimens of *T. quadrisignata* deposited in the private and public collections with reliable labels are from within the distribution area published by Pillet. Interestingly one voucher from Stalden (Visp Valleys) was determined correctly in the 19th century (1883, det. Lethierry, NHBE). According to museum collections many specimens have been captured in this region. Our distribution map reports all voucher specimens, recent acoustic recordings and visual observations. Furthermore, Pillet's records were assessed as being valid if they originate from spatial unities where the suspicion on an occurrence of *T. steveni* is very low.

ECOLOGY AND THREAT

Tibicina quadrisignata is a specialized species in Switzerland. It lives in very xerothermic habitats with a mosaic of scattered Scots Pine (*Pinus sylvestris*) and Savin Juniper (*Juniperus sabina*), sometimes entering dry pine forests. Singing has been observed on ten different woody plants (Pillet, 1993). Comparable habitats are occupied in the Aosta Valley. In contrast, southern French populations are most abundant in woodland ("lande haute fermée", "bois"; Puissant, 2006). Therefore, the Swiss and adjacent Italian populations possibly form a specialised ecotype.

The national threat to *T. quadrisignata* results from the following facts: the small distribution area within Switzerland, the low population densities typical of the genus, the spatial isolation at the north-eastern border of the distribution area, the stenoeccious habitat requirements and habitat loss by artificial irrigation and expansion of vineyards or settlements. Moreover, the general international rareness of both the species and the specific ecotypes increase the necessity for the conservation of the species at the Swiss level. *T. quadrisignata* is an attractive flagship species for the driest habitats of the country and could be highlighted in nature conservation programs.

Tibicina steveni (Krynicky, 1837)

German common name: Gelber Scherenschleifer

French common name: La Cigale de Steven (Puissant, 2006)

The German name has been formed similarly to *T. quadrisignata*. It is the only species of the genus with yellow marks on the mesonotum, a broad yellow stripe at the posterior margin of the pronotum and with a yellow coloration of the basal wing venation in Central Europe.

DISTRIBUTION (Fig. 6)

Tibicina steveni was originally known as an eastern Mediterranean cicada. It was described from the Taurus Mountains (Turkey) and is distributed in Azerbaijan, Armenia, Georgia, Ukraine (Crimea) (Sueur *et al.*, 2003) and Bulgaria (Gogala *et al.*, 2005). The occurrence in Switzerland and in one place in France was unexpected

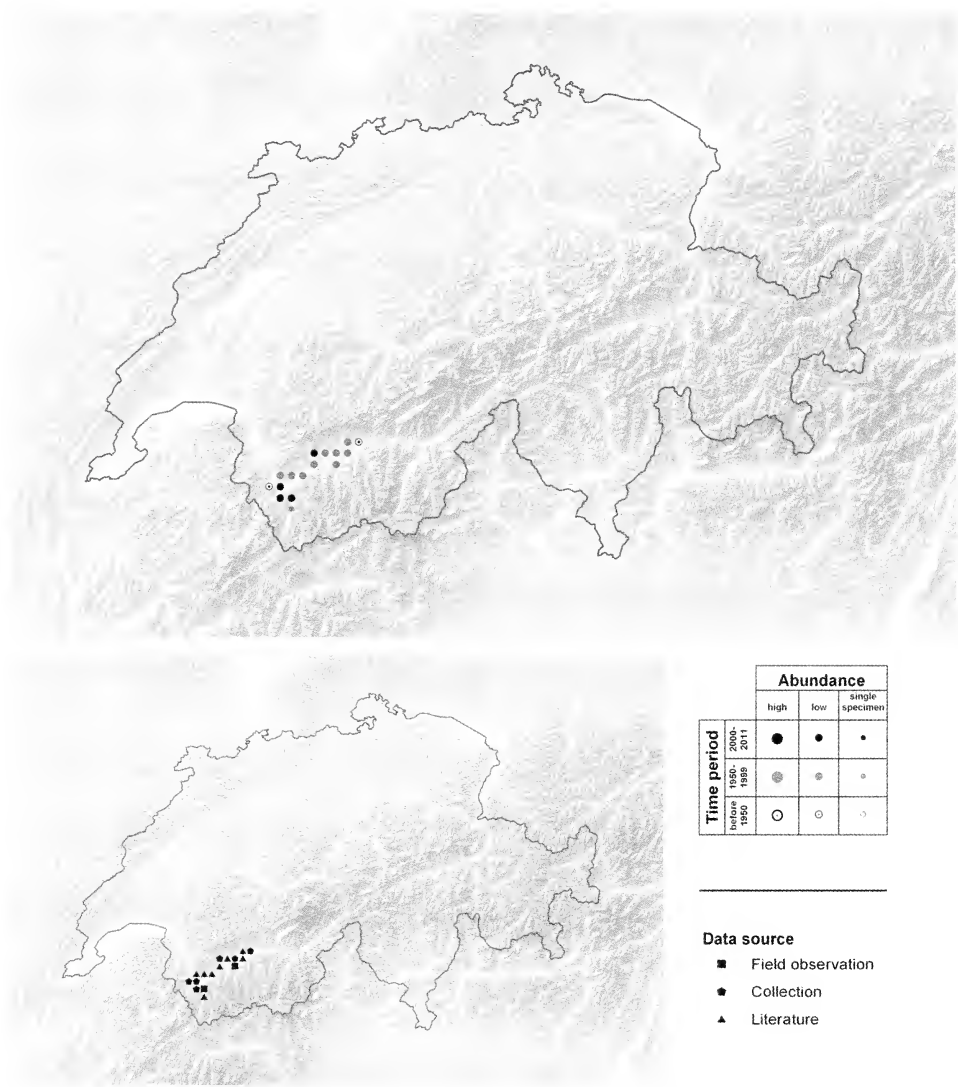


FIG. 6
Distribution map of *Tibicina steveni* (top) including the data source for the records presented (below).

(Sueur *et al.*, 2003). It has recently also been found in a wider but fragmented range in the northern Apennine Mountains in Italy (pers. data).

Swiss populations of *T. steveni* have actually been known as “*Cicada sanguinea*” for more than 150 years (Bremi in Hagen, 1855). He estimated that the species was not rare in the Valais, although less abundant than *C. orni*, but he had probably included observations of *T. quadrisignata* in his assessment. Judging by nine specimens caught between 1891 and 1899 and preserved in different public collections

(NMBE, NMLS and NMS), the species must have occurred fairly frequently in the Martigny region (VS) at that time. Farquet's (1940) "*C. haematodes*" at Mont Ravoire near Martigny must be *T. steveni* and is the only detailed chorological information published before Pillet (1993).

Tibicina steveni only occurs in the western parts of the Rhone Valley (VS) and a few of its side valleys (Pillet, 1993). Some of the records made by Pillet are doubtful since *T. quadrisignata* has been reported from the same site subsequently (see previous section). For that reason the exact distribution area has to be reinvestigated for the western part of the Valais. Specimens from collections labelled with "Aïre" (GE, MHNG), "Peney" (GE, MHNG) and "Clarens" (VD, NMBE), all of them far away from the known distribution area, we suppose to be erroneous. The first two (Aïre and Peney) were reported by Maerky, who is known to have mixed up localities when labelling specimens. Moreover, the Peney label originates from Tournier, who was also an insect dealer (Hollier, pers. comm.). The third (Clarens) is without any further information, but there is also a specimen of *Tibicina quadrisignata* preserved in the same collection and with the same handwriting from this site and it is probable that there have been labelling errors.

Sueur *et al.* (2003) hypothesized that the Swiss and French populations must be a relict of a formerly wider distribution of the species across Europe. We support this opinion based on the following considerations: The hypothesis of a relictual occurrence in the western part of the distribution is verified by the recent observations in Italy, isolated populations are common for the Valais with its characteristic dry climate, and the biogeographical pattern with the main distribution area in the East (Europe and/or Asia minor) is not unique for species occurring in the Valais. Delarze (1987) has published a list of 21 beetles, two grasshoppers and one spider occurring in the Valais that are at least more abundant in Eastern Europe than in the Rhone Basin. He discussed the origins of the xerothermic flora and fauna and concluded that a colonisation of the Valais along the Jura Mountains and north of the Alps could not be excluded for some oriental insects since the late glacial period.

ECOLOGY AND THREAT

Tibicina steveni is a stenoeccious species preferring dry Scots Pine tree forests (= *Ononido-Pinion*, see Delarze & Gonseth, 2008) and oak woods (*Quercion pubescenti-petraeae*). The species inhabits closed habitats (Sueur *et al.*, 2003). Singing males are often observed sitting on Scots Pine (*Pinus sylvestris*) or on Downy Oak (*Quercus pubescens*) (Pillet, 1993). Sometimes they also sing in neighboured vineyards.

A good knowledge of the distribution and ecology of this attractive species is essential, because Switzerland is exclusively responsible for the conservation of the Central European populations. The population densities are low, the occurrence isolated and restricted to a very small area. Pillet (1993) already pointed out the severe threat especially due to the continuous expansion of the vineyards. Similar to *T. quadrisignata*, this species is a perfect model for flagship species concepts in nature conservation.

***Tibicina haematodes* (Scopoli, 1763)**

German common name: Weinzirner (e.g. Schedl, 2000)

French common name: La Cigale rouge (e.g. Boulard, 1995)

DISTRIBUTION (Fig. 7)

All studies reporting *Tibicina haematodes* from the Valais are considered to be incorrect (Fuesslin, 1775; Stoll, 1901; Kuntze, 1931; Schedl, 2000) as well as two voucher specimens labelled with “Wallis” (NMT) and “Martigny” (VS, MNHN). Nevertheless, it is possible that the species could have reached Switzerland from three different directions historically, from the north, the south or the west, since it has been published for all neighbouring countries except Liechtenstein: Italy [up to Bozen (Schedl, 2002) and around Torino (Griffini, 1896; Della Beffa, 1925)], France [including central parts (e.g. Hagen, 1855; Puissant, 2006)], Austria [Vienna region (e.g. Hagen, 1855; Wagner & Franz, 1961; Schedl, 2002)] and Germany [Rhine-Main region (e.g. Hagen, 1855; Vogel, 1935, 1937; Schwoerbel, 1957)].

With respect to the north, Labram & Imhoff (1845) mentioned *T. haematodes* as a very rare species in the Basel region. One historic population is mentioned from the vineyards in Rouffach (Alsace, France) situated only 50 km north of Basel (Döderlein, 1913; Huber, 1916). 16 specimens of this time are deposited in the collection of the Zoological Museum of Strasbourg labelled with the nearby village of Westhalten (Hugel *et al.*, 2008). The German population nearest to Switzerland was described from Tübingen (Baden-Württemberg) with a population of 80 to 100 specimens (Schwoerbel, 1957). Fischer (1847) cited an occurrence from Tuttlingen and Immendingen (Baden-Württemberg) that is only situated 15 km north of the Swiss border, but had doubts about the identification. To summarize, it is possible that Labram & Imhoff (1845) are correct and *T. haematodes* had sporadically occurred in the Basel region, but nevertheless it is more likely that the authors confused it with *C. montana* s. l. A specimen labelled “Winterthur” (ZH) (1900-1910, leg. Huber, NMWI) is considered as doubtful, since it was near a handwritten label with “cicada from the Mediterranean for comparison”. The location probably refers to the domicile of the collector.

With respect to the south, no reliable historic references could be found that *T. haematodes* once occurred in Ticino. Two unlabelled specimens are deposited in the MCSN collected by Scherrer and Maestri who were active mainly in southern Ticino and especially in the surroundings of Morcote and Melide at the beginning of the 20th century (Pollini Paltrinieri, pers. comm.).

Vernier (1996) mentioned a historical occurrence of the species for the Geneva region, the most western part of Switzerland. In fact, six adult specimens (1 ♀, 5 ♂) and four nymphal skins of *T. haematodes* from the Canton of Geneva are preserved in the collection of the MHNG. They are labelled from the two localities “Pont Butin/Aïre” (western city limit of Geneva) and “Nant de Lagnon” (east of Aire-la-Ville, municipality of Bernex) (leg. Simonet, Schauenberg, Maerky or anonymous). We therefore conclude that a reproductive population must have existed along a four kilometre length of the Rhone River from 1914 to 1947.

Despite recent intense field work, *T. haematodes* was found neither in southern Ticino nor in the Basel region. When investigating the slopes of the Rhone River

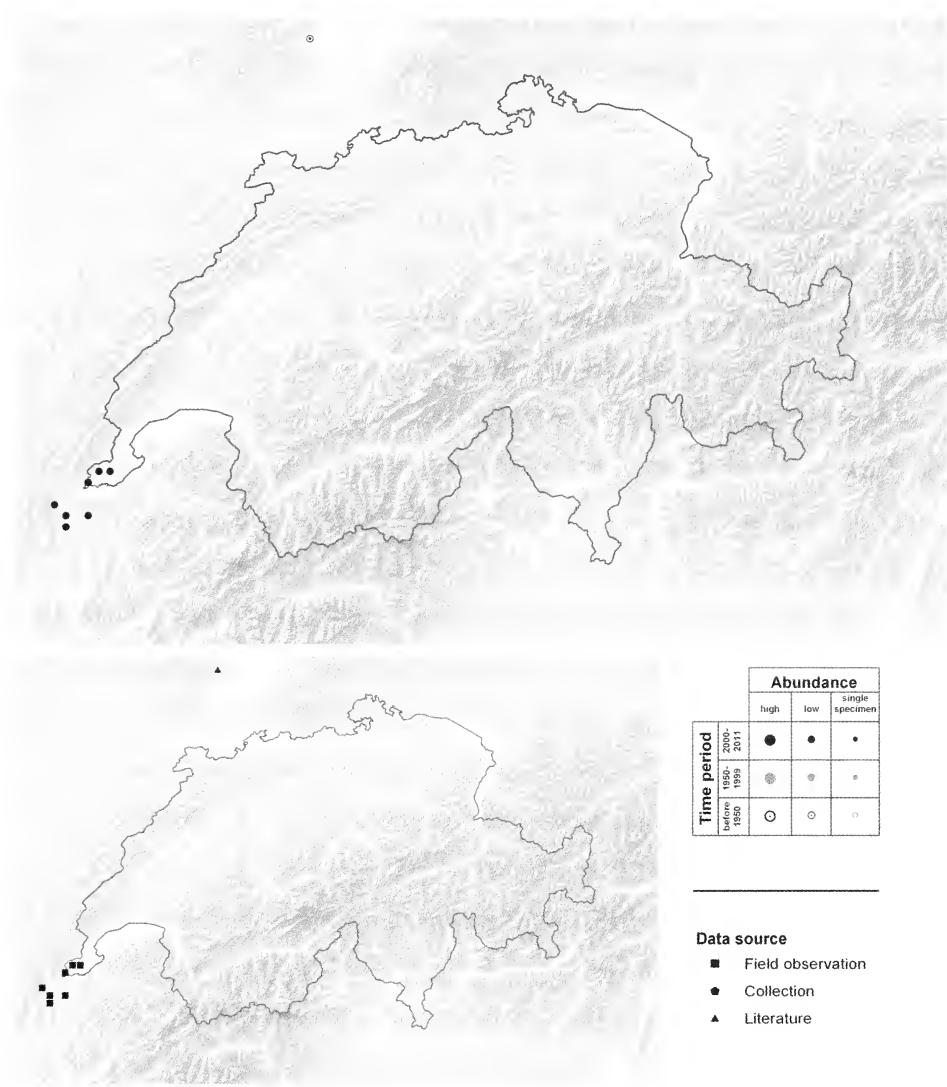


FIG. 7

Distribution map of *Tibicina haematodes* (top) including the data source for the records presented (below).

downstream of Geneva two small populations of 3 to 4 singing males each were discovered at the historically known localities Pont Butin and Nant de Lagnon in 2012 and a single singing specimen was discovered at Cartigny (GE) in 2011 and in 2012. These are the first known observations of the species for more than 60 years in Switzerland.

ECOLOGY AND THREAT

The historic and recent Swiss habitats in the Geneva Region are oak dominated deciduous woodland on steep slopes. At the Pont Butin locality two specimens entered

a small orchard in 2012. An occurrence in vineyards is not documented for Switzerland. The site Pont Butin/Aïre seems to be adversely affected by settlements. The Rouffach population (Alsace, France) was endangered through the collecting of this attractive species by dealers (Döderlein, 1913).

Tibicina haematodes is an indigenous, but extremely rare Swiss species. The current population size is about 10 calling males. It is interesting that we have found the species 60 years after the last record at exactly the same localities. Either the two small but striking populations have been continuously present without any public recognition or the species has re-immigrated to its former habitats. The population in the Val des Usses (Haute-Savoie, France) mentioned by Vernier (1996) is still present according to regular observations until 2010 (Bal, pers. comm.). Given its short distance of only 15 km from the Swiss border, it might serve as a pool for immigration. With the rise of more ecologically sensitive approaches to viticulture, supported by a milder climate, *T. haematodes* might be establish more numerous populations in Switzerland. Nevertheless, the species is currently critically endangered.

***Cicadetta montana* s. str. (Scopoli, 1772)**

German common name: Pechader-Bergzikade (Hertach, 2010)

It seems obvious to keep the well-established name “Bergzikade” (= Mountain Cicada) and add a prefix for all species of the complex in order to demonstrate their close relationship. *Cicadetta montana* s. str. often can be distinguished from all other Central European species of the clade by its black or very dark coloured basal wing venation (“Pechader” = pitch coloured venation).

DISTRIBUTION (Fig. 8)

It is difficult to present a historical overview of the distribution of *C. montana* s. str., because until 2004 only records referring to the whole species complex have been published, with the exception of one record by Artmann (1987). Nevertheless, we report here some historical data for *C. montana* s. l. with special focus on records originating from regions where only *C. montana* s. str. is expected although these are not presented on the map.

In a coloured figure Sulzer (1761) drew an accurately shaped *C. montana* s. l. but named it *C. orni*. He did not provide any Swiss localities. Referring to this drawing, Fuesslin listed the taxon for Leuk (VS, Sierre region). Heer & Blumer (1846, p. 210) published a sporadic occurrence up to the “Wart” for the Canton of Glarus at “2000 feet” (≈ 600 m a.s.l., probably near Schwanden in the Sernf Valley). They call the species erroneously “Blutcicade (*Cicada haematodes*)”, but the presence of *T. haematodes* can be reliably excluded from this region because of its harsh climatic conditions. Breimi (1849, Breimi in Hagen, 1856b) gives the most complete overview on the occurrence in the middle of the 19th century stating that the species is widespread but not common in warm lowland areas including the Zurich region, and that it was found at high altitude locations near a glacier in the Valais. The following further sites have been published: Glarus and Bern (Milde, 1866), a few exactly described places in the Canton of Zurich (Dietrich, 1872; Stoll, 1901), in the lower parts of the Engadine Valley (GR) (Hofmänner, 1924; Günthart, 1987) and in the Finges Forest (VS) (Bille, 1980; Artmann, 1987). Pillet (1993) published a detailed map of the Valais populations.

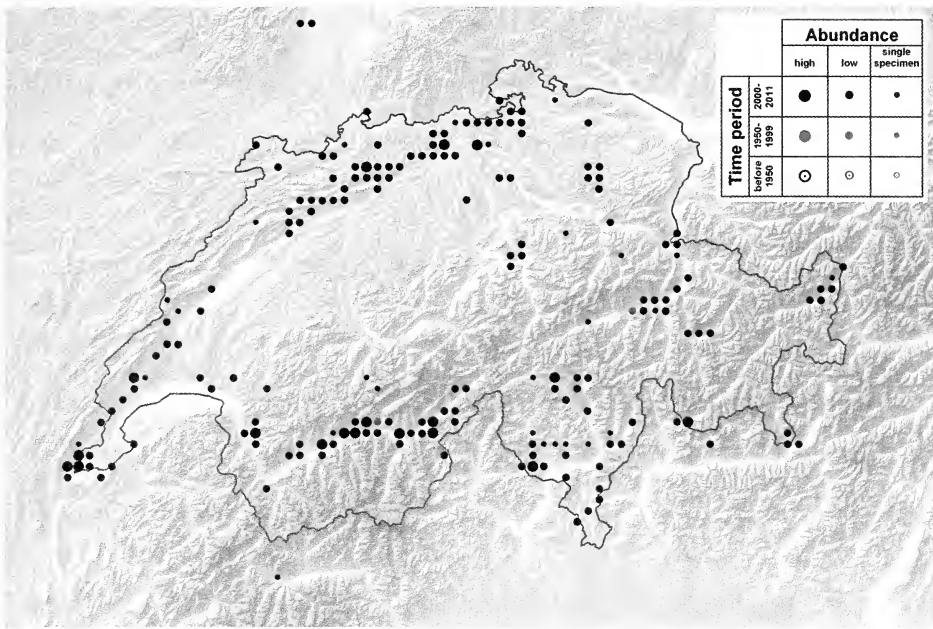


FIG. 8

Distribution map of *Cicadetta montana* s. str. including solely acoustically checked records.

But since a second species of the complex occurs in this region, conclusions are difficult to reach and his data could unfortunately not been integrated into our map. Notable older voucher specimens for regions which are not well represented in the map, but probably only with this single species, originate in chronological order from Weissenburg (BE) (1849, NAAG), Frauenfeld (TG) (1892 and 1904, NMT), Gerzensee (BE) (1915, NHMB), Erstfeld (UR) (1916, NAAG), Davos Monstein (GR) (1935, ETHZ), Röthenbach i. E. (BE) (1961, NMBE), Hagneck (BE) (1979, NMBE), Isenthal (UR) (1986, NMLS) and Warth-Weiningen (TG) (1997, NMT).

In Switzerland, *C. montana* s. str. is by far the most widely distributed species, although scarcely observed even by many entomologists. The previously published map (Hertach, 2007) has now been complemented with new records mainly from northern Ticino, Grisons and the Lake Geneva Basin. *C. montana* s. str. occurs in almost all regions of Switzerland but is very rare in the hilly Swiss Plateau. In the entire Grisons except for the Mesocco Valley and for the Poschiavo Valley, in the northern Prealps (Nördliche Voralpen) and in northern Ticino it is the only representative of the family Cicadidae. In the Valais, the most elevated population is established up to 2010 m a.s.l. (Rosswald; Hertach, 2007), which as far as we know has not been surpassed by any other Central European Cicadidae.

ECOLOGY AND THREAT

The habitat requirements of this and the other three species in the *C. montana* complex have been described in detail (Hertach, 2007). The rather broad habitat

requirements have been confirmed within the last years, with a clear preference of sparse Scots Pine (*Pinus sylvestris*) woodlands and dry to mesophilous ecotone habitats. This species is the most difficult to observe due to its preference for singing in the treetops in combination with its rather faint almost ultrasonic song.

The species has probably suffered due to habitat loss in the hilly Swiss Plateau judging by the description of Brems (in Hagen, 1856b) and some of the sites given by Dietrich (1872). In Ticino, suitable habitats have been lost by the abandonment of traditional land use. Nevertheless, *C. montana* s. str. is widely distributed and currently only locally endangered. The European distribution is large but we do not know of other regions with comparable population densities. It is rare in the Italian Alps. Therefore, we assume that Switzerland has a responsibility for the conservation and maintenance of large populations of this species. *C. montana* s. str. benefits at warm and sunny sites by thinning out forests on poor soils (especially pine forests) and by improving the structure of forest edges near dry and semidry meadows. Such measures have been conducted by regional authorities over the last decades.

Cicadetta cantilatrix Sueur & Puissant, 2007

German common name: Honigader-Bergzikade (Hertach, 2010)

Cicadetta cantilatrix can often be distinguished from *C. montana* s. str. by a yellow to brown colouration of the basal venation of the fore wing ("Honigader" = honey coloured venation).

DISTRIBUTION (Fig. 9)

C. cantilatrix was described very recently and separated from *C. cerdaniensis* by acoustic characters (Sueur & Puissant, 2007a). For the acoustic description Sueur & Puissant integrated recordings from Switzerland (Martigny-Combe, VS), but the holotype and paratype were collected in France. The taxon has been discussed critically due to intermediary song patterns observed several times in northern Switzerland (Hertach, 2007). These intermediary song patterns are now interpreted as courtship songs of *C. cantilatrix* (Trilar *et al.*, 2006; Hertach, 2011) which are very close to the calling songs of *C. cerdaniensis*. Therefore, *C. cantilatrix* is a valid species (Hertach, 2011).

It is possible that Brems (1849) and his German colleague Siebold already knew about this species. There is an older reference to a population in Diegten (BL, Jura Mountains; Artmann, 1987) where the species is still present and frequent. *C. cantilatrix* is not rare in Switzerland and it is surprising that it was not detected earlier (Hertach, 2007). It is well distributed in the Jura Mountains including the Randen massif in the east and entering to the eastern part of the hilly Swiss Plateau. We have found 17 local populations solely in the Canton of Aargau, some of them abundant. It also occurs quite regularly in the lower Valais and in the Chablais (VD). The main distribution is split into two big disjunct metapopulations in Switzerland (Jura and Chablais/Valais). Additionally, there are three supposedly isolated local populations: Immenberg (TG, discovered by Keist), Uetliberg (ZH, discovered by Rey) and Epesses (VD).

ECOLOGY AND THREAT

C. cantilatrix is specialized on sparse Scots Pine forests with a grass-rich understorey on marl (= *Molinio-Pinion*, see Delarze & Gonseth, 2008) and variable

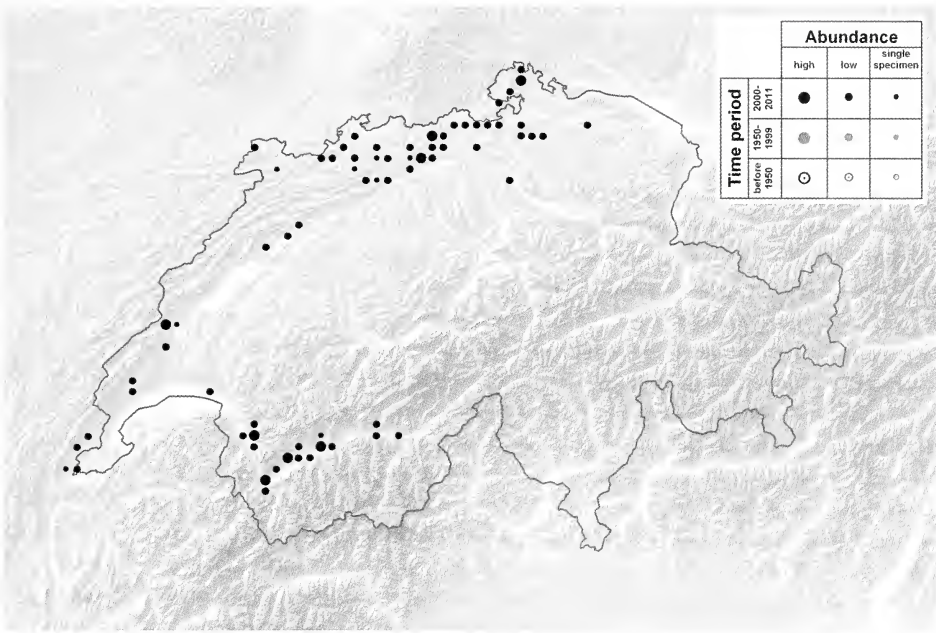


FIG. 9

Distribution map of *Cicadetta cantilatrix* including solely acoustically checked records.

edges of the forest along extensively used semidry meadows normally with Upright Brome (*Bromus erectus*) (= *Mesobromion*, see Delarze & Gonseth, 2008) in the Jura Mountains and in the Chablais and on sparse woods with Downy Oak (*Quercus pubescens*) in the Valais (Hertach, 2007). In contrast to *C. montana*, it scarcely occurs on rocky cliffs and ridges. It is a stenoeious species whose abundance is often correlated with nature conservation measures and traditional land use.

Beyond Switzerland, the distribution area is large, but a comparable abundance is not known. It therefore seems that the Swiss responsibility for its conservation is high. As in *C. montana* s. str., it benefits from recent improvements of suitable habitats (Hertach, 2007). The very active role of cantonal authorities in thinning out pine forests might create an important positive factor for the current frequency in the Cantons of Aargau and Basel-Land.

Cicadetta sp. aff. *cerdaniensis* Puissant & Boulard, 2000

TAXONOMY

Cicadetta cerdaniensis was described recently as an endemic species from the Pyrenees (Puissant & Boulard, 2000). A taxon with a very similar song pattern occurs in Italy and the southernmost parts of Switzerland (Hertach, 2007; Trilar & Hertach, 2008; Hertach, 2011; Hertach & Pollini Paltrinieri, 2012). During the last years we have gathered much data on acoustic, morphologic and genetic characters and the spatial distribution from many locations across the whole range of this taxon. This will allow a better taxonomic understanding.

DISTRIBUTION (Fig. 10)

The Swiss distribution of *C. sp. aff. cerdaniensis* is well known. In the Lugano region, the species is the most common representative of the *C. montana* complex but there are only nine local populations. The Monte San Giorgio (TI) population is one of the most numerous of the Alps (up to 50 singers). Additionally the species was found north of Monte Ceneri (TI) three times with isolated singers (Castaneda, GR, Juillerat, pers. comm.; Gudo, TI; Tegna, TI). The location in Castaneda (Mesocco Valley, GR) might be a reproductively viable population.

ECOLOGY AND THREAT

Cicadetta sp. aff. cerdaniensis is specialized on sunny and sparsely vegetated woodland (*Orno-Ostryon*) and semidry meadows with shrubs or forest edges in Switzerland. Similar to *C. cantilatrix*, this species prefers low trees and bushes when singing. Almost all habitats are situated on calcareous soils.

The species probably already suffered in the Celto-Latin period, when early settlers transformed open deciduous woodland into forests of European Chestnut (*Castanea sativa*) (e.g. Hegg *et al.*, 1993). A serious decline may have taken place after the abandonment of semidry meadows and the expansion of settlement areas in the last century. These last two adverse processes have been mitigated but not stopped by nature conservation measures and stricter land use planning regulations. *C. sp. aff. cerdaniensis* is endangered in Switzerland.

***Cicadetta brevipennis* Fieber, 1876 (*sensu* Gogala & Trilar, 2004)**

German common name: Gras-Bergzikade

French common name: La Cigalette à ailes courtes (Puissant, 2006)

The common German name is derived from an unusual behaviour within Central European cicadas: *Cicadetta brevipennis* is regularly singing in the herb layer ("Gras" = grass).

DISTRIBUTION (Fig. 11)

Historic records of this forth member of the *C. montana* species complex can not be reported. It is the rarest species within the complex in Switzerland, but the most frequent in the Mediterranean parts of France (Puissant, 2006) and in some parts of Slovenia (Gogala, pers. comm.).

The distribution area reaches Switzerland in the Geneva region and southern Ticino. Not more than two populations and an isolated calling male are known from Ticino, but the population on Monte San Giorgio is very numerous with more than 100 calling males. The Ticino populations are not well interconnected with Italian ones. *C. brevipennis* has its most important Swiss populations along slopes of the river Rhone in the Canton of Geneva. Furthermore, an isolated population was discovered in the Orbe region in 2011. The Alsace populations (Hugel *et al.*, 2008 and pers. data) do not reach the Swiss border from the north.

ECOLOGY AND THREAT

C. brevipennis resembles *C. sp. aff. cerdaniensis* in habitat selection in Ticino and it can occur syntopically with the latter. The composition of the woody plants is

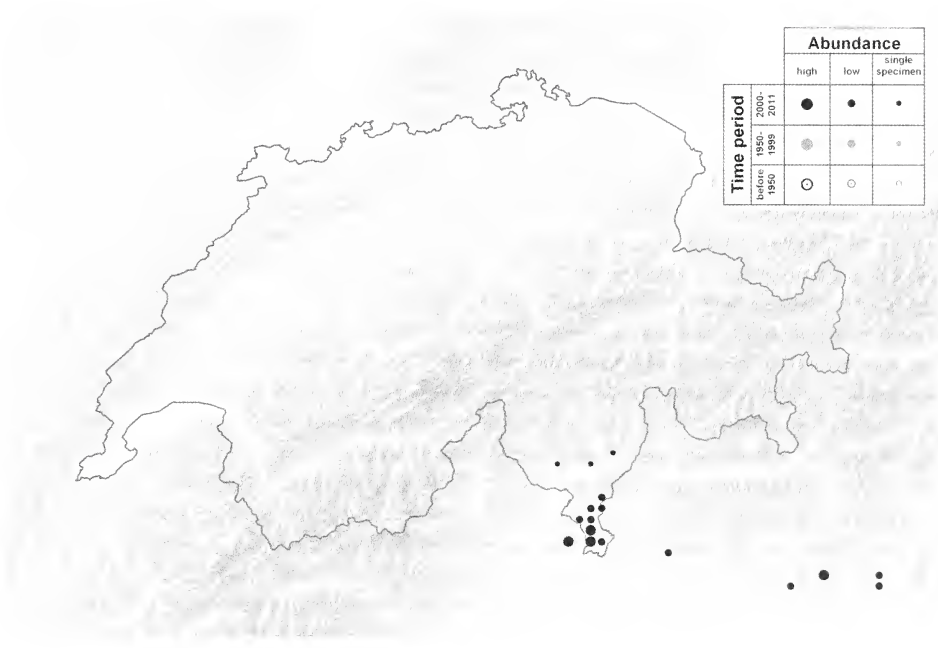


FIG. 10

Distribution map of *Cicadetta* sp. aff. *cerdaniensis* including solely acoustically checked records.



FIG. 11

Distribution map of *Cicadetta brevipennis* including solely acoustically checked records.

similar, but *C. brevipennis* prefers more open ecotone habitats with a tendency to semidry meadows. In the Canton of Geneva, *C. brevipennis* more or less replaces *C. cantilatrix* in sparse Scots Pine forests (*Pinus sylvestris*) and ecotone habitats with a slight preference for drier soils. For more ecological data see Hertach (2007).

The species is stenoeccious and endangered by the abandonment of traditional land use and by grazing or intensification of semidry or dry meadows, especially in Ticino and at the location near Orbe. The national conservation importance of this species for Switzerland is less relevant given its wider distribution in other countries. Nevertheless, Swiss populations do not seem to be connected with large populations, at least not in Italy, and their genotypes may therefore differ from the core distribution of the species.

***Tettigettalna argentata* (Olivier, 1790)**

German common name: Silbrige Zikade (Gogala, 2002)

French common name: La Cigalette argentée (e.g. Boulard, 1995)

DISTRIBUTION (Fig. 12)

Tettigettalna argentata (Olivier, 1790) is a small western Mediterranean cicada species that has been recorded in Spain and Portugal (Sueur *et al.*, 2004), France (Puissant, 2006), northern Italy (Ferrari, 1892; Schedl, 1973, 2000) and western Slovenia (Gogala & Gogala, 1999). Some of the records of Schedl (1973) are situated not far from the Swiss border. The occurrence near Meran in the Italian South Tyrol had already been detected and described in the middle of the 19th century (Milde, 1865).

Tettigettalna argentata was discovered for the first time in Switzerland at Monte Caslano (TI, Lugano region) in 2007 (Hertach, 2008). The species is abundant there with more than 30 males singing in 2008.

No other populations have been found in Switzerland, but a single and supposedly immigrant specimen was observed and recorded near San Vittore (GR) in the Mesocco Valley on 29 July 2011. Other current populations nearly reach the Swiss border in different regions: 1.7 km from the Poschiavo Valley (GR) (Tirano, 2010 and 2011), 10.4 km from the Valais (Doues, Aosta Valley, 2007) and 29.5 km from the Val Mustair (GR) (Kastelbell-Latsch, Vinschgau, 2009). Immigration into the Poschiavo Valley might be expected in the near future.

ECOLOGY AND THREAT

The habitat at Monte Caslano consists of a very steep and rocky slope on limestone (*Orno-Ostryon*). Some areas of Monte Caslano are cultivated as dry meadows with bushes and small woods for habitat conservation by regional authorities (Hertach, 2008). Maintenance or slight extension of these activities seems to be crucial for the conservation of this population of *T. argentata*. The Mesocco Valley specimen sang in intensively cultivated land with a garden, hedges and pastures, which is not typical for the species.

With only one established population the occurrence of this species in Switzerland is endangered. Nevertheless, the responsibility for the species is not high in the international context.

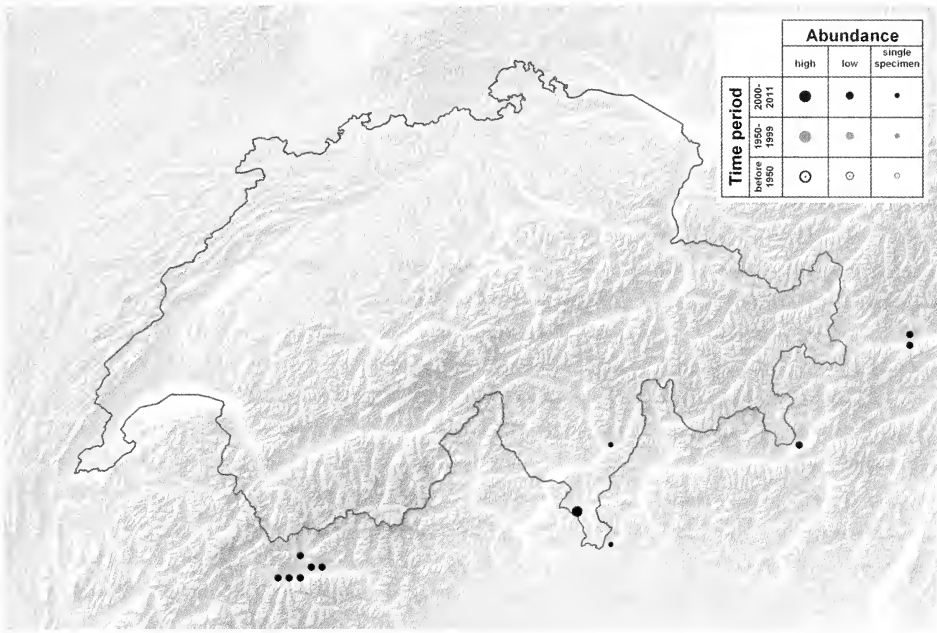


FIG. 12
Distribution map of *Tettigettalna argentata*.

COMMENTS ON OTHER SPECIES

Cicadatra atra (Olivier, 1790)

Bremi (1849) named the most frequent Swiss species “*Cicada concinna*”, which, according to this description, must be assigned to *Cicadetta montana* s. l. Some authors classify *Cicada concinna* Germar, 1821 as a synonym of *Cicadatra atra* (e.g. Hagen, 1855; Fieber, 1876; Metcalf, 1963). Bremi was therefore probably misinterpreted as his record of “*Cicada concinna*” seems to have lead several authors to the conclusion that *C. atra* is a Swiss species: Haupt [1935, “reaching the southern parts of Switzerland (Valais)”], Robert (1937, “more abundant than *C. orni*, *L. plebejus* and *T. haematodes* in Central Europe”), Metcalf (1963), Nast (1972, 1987), Schedl (2000, “southern Switzerland”, the symbol in the corresponding distribution map is located in the Valais), Holzinger *et al.* (2003) and Hoch (2011). Neither historic nor recent evidence could be found in collections or in the field. It is rather unlikely that *C. atra* has occurred in Switzerland. The nearest recent observations are situated in the Mediterranean parts of France (Puissant, 2006) and in the most northern Apennine Mountains (pers. data). Servadei (1967) did not mention of Italian records north of the Emilia Romagna.

Tibicina nigranervosa Fieber, 1876

Puton (1899) listed *T. nigranervosa* for Switzerland, Spain and Corsica. Nast (1972) followed him and added Portugal (and Russia). Both most probably mistake

T. nigronervosa for *T. quadrisignata* in Switzerland. Incorrect labels reflecting the same confusion have been found in collections (e.g. Salgesch, 1889, BNM). Nast (1987), obviously aware of his mistake, eliminated *T. nigronervosa* from the second list for Switzerland. *T. nigronervosa* is currently known to occur as an endemic species in Corsica and Sardinia (Puissant, 2006). It is considered to have never been native to Switzerland.

***Saticula coriaria* Stål, 1866**

Saticula coriaria is a northern African species (Boulard, 1981), which has been listed for Switzerland tentatively but erroneously by Fieber (1876) and later by Nast (1972). The confusion started with “*Cicada violacea*, die Blaue” reported from Geneva by Fuesslin (1775) and referring to *Cicada violacea* Linné, 1758 which is actually not a European species. Boulard (1981) demonstrated in detail that several authors concluded erroneously the two taxa mentioned to be in synonymy. We are unable to speculate to which species Fuesslin was referring to.

***Cicadivetta tibialis* (Panzer, 1798)**

This very small cicada is one of two species that could expand their distribution areas towards Switzerland supported by global warming in the future. The species has been described and later listed by Wagner & Franz (1961) and by Schedl (2002) for the Vienna region, which is climatically comparable to some parts in Switzerland. The nearest, spatial occurrences are reported from the Lake Garda region (Schedl, 2002 and pers. data) and from the Piedmont (Novi Ligure; Ferrari, 1892).

***Tettigettula pygmea* (Olivier, 1790)**

syn. *Cicadetta brullei* Fieber, 1876

Tettigettula pygmea (*sensu* Puissant & Sueur, 2010) is very widespread and frequent in central and southern Italy, reaching elevated locations in the mountains. Because of its nearly ultrasonic song it is probably often missed. Servadei (1967) reports this species from Lombardy, unfortunately without specifying a more precise locality. Schedl (2004) mentions a single voucher specimen found at the Lake Neusiedl region in 1973. He has never listed the species for the south-eastern Alps (Schedl, 1973, 2000), but we have found it for example at Monte Collalto (Bassano di Grappa, Veneto). This is currently the nearest location to the Swiss border and an expansion towards the Ticino region would not be surprising.

***Platypleura kaempferi* (Fabricius, 1794)**

A single male of this common Japanese species (Hayashi & Saisho, 2011) has been captured in a garden from Gland (VD, Lake Geneva Basin) on 20 August 2011 after having already sung the previous evening (leg. Delapierre, det. Duffels/Boulard/Hayashi). *Platypleura kaempferi* is certainly not a species native to Switzerland and must have been introduced by human activity. There is a garden centre selling exotic trees within 200 metres of Gland locality, and we suppose the specimen to have been introduced with root balls in a larval stage. Furthermore, we assign song recordings made in a settlement in Jegenstorf (23.8.2003; Cordillot, pers. comm.) to another exotic but currently undeterminable cicada.

DISCUSSION

Due to detailed fieldwork and the use of bioacoustic methods, the number of cicada species in Switzerland has been doubled within the last few years. Pillet (1993) included five species; now we are able to present ten species as certainly indigenous. It is likely that none of these species has immigrated recently. The ten species recorded from Switzerland demonstrate the transition between the northern regions harbouring only few species (e.g. Germany: 5 species, Nickel & Remane, 2003; Meineke, 2012) and the southern regions rich in species (e.g. France: 20 species, Puissant, 2006; Puissant & Sueur, 2011; Macedonia: 15 species, Gogala *et al.*, 2005; Portugal: 13 species, Sueur *et al.*, 2004). Similar species numbers have been published for the equally well studied countries Austria (8 species, Schedl, 2002, Schedl, 2004; Trilar & Holzinger, 2004) and Slovenia (11 species, Gogala & Gogala, 1999; Gogala & Trilar, 2004). Four of the five largest European species are present in Switzerland, and five of the ten native species have impressive songs. The *Cicadetta montana* species complex is well represented with four species. For comparison, three species have been published for Austria (Trilar & Holzinger, 2004) and Germany (Meineke, 2012), and five for France (Sueur & Puissant, 2007a, b). Many species reach Switzerland only marginally, *Tettigettalna argentata* and *Cicadetta* sp. aff. *cerdaniensis* from the South, *Tibicina haematodes* from the West and *Cicadetta brevipennis* and *Lyristes plebejus* from the South and West. Swiss national responsibility for the conservation of these species is not high in an international context. In contrast, the isolated populations of *Tibicina quadrisignata* and *T. steveni* are potentially good flagship species with a high international responsibility for their conservation (Fig. 15). The abundant local populations of *Cicadetta montana* s. str. and in particular *C. cantilatrix* are important and, at least until comparable data from elsewhere is available, must be assumed to result in a high national responsibility for their conservation.

We demonstrate that some species which have been published for Switzerland in previous works should be omitted from the species list (*Cicadatra atra*, *Tibicina nigronervosa*, *Saticula coriaria*). We also publish a record of an exotic Asian cicada species (*Platypleura kaempferi*) found in Central Europe for the first time. Such incidents are rare since adult specimens appear to die within a few days without suitable nutrition.

Three parts of the country are clearly important with respect to the regional diversity of species: The Valais (e.g. Pillet, 1993), Ticino and more surprisingly the Lake Geneva Basin (Fig. 13 and 14). The grid cell "Sierre" is the only one with five species occurring. 15 cells with four species detected are situated in the Valais (9), Ticino (3), the Canton of Geneva (2) and Grisons (1). Up to four species are associated syntopically in the Lugano region (TI) and parts of the Rhone Valley (VS). The Jura Mountains and especially the eastern parts in the Cantons of Aargau and Basel-Land are recognized as of international importance for their numerous *Cicadetta cantilatrix* populations. Populations of three species in the *C. montana* group occur within a distance of a few kilometres in the Canton of Geneva as well as in the Lugano (TI) and Orbe (VD) regions. An almost deafening concert of dozens of calling males for example of *L. plebejus* and *C. orni* between Gandria and Castagnola (TI, Lugano region) possess an additional value. At these locations natural acoustic spectacles can

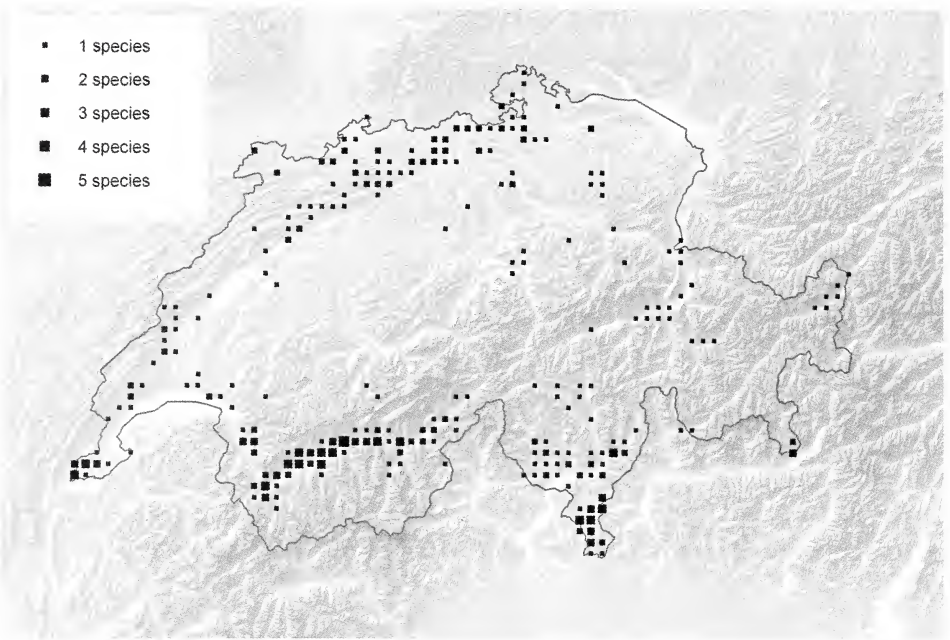


FIG. 13

Species number for each grid cell showing the centres of species diversity.

be found that may only be surpassed in power by a chorus of European Tree Frog (*Hyla arborea*) or Natterjack Toad (*Bufo calamita*) in Switzerland. The potential of this experience should be used for nature education in a country more and more dominated by artificial sounds and noises.

Nine of the ten species are critical with respect to the ecological quality of their habitats (Fig. 15). *Cicada orni* is the only species that has been recorded several times in man-made habitats such as parks or gardens. Favourite habitats for Swiss cicadas consist of different oak and pine forests and traditionally used semidry and dry meadows with bushes and trees. They are often restricted to scattered locations on the driest, poorest soils and the sunniest exposures. The plant association (*Orno-Ostryon*) characterized by Downy (*Quercus pubescens*) and Turkey Oak (*Quercus cerris*), Hop Hornbeam (*Ostrya carpinifolia*) and Manna Ash (*Fraxinus ornus*) in Ticino and xerothermic habitats with Scots Pine (*Pinus sylvestris*), Savin Juniper (*Juniperus sabina*) and/or Downy Oak in the Valais form very important habitats. Apart from local climatic conditions, habitat structure is more important for species of the *C. montana* group than for any other species. These species prefer ecotone habitats or open woodlands with a well-developed herb layer.

A clear decline in population numbers and distribution area can be documented for *L. plebejus*, which has become extinct in the Valais (Pillet, 1993; Keim, 1999). Other species have probably suffered locally due to habitat loss. Considering Breimi (in Hagen, 1856b) and Dietrich (1872), *C. montana* s. str. and *C. cantilatrix* supposedly



FIG. 14

Centres of cicada diversity: Four syntopically occurring species at Lintellière (central Valais, left), three species of the *C. montana* group within a few square kilometres at Denti della Vecchia mountains (Lugano region, TI, right) and up to five regularly and irregularly observed species at slopes of the Rhone river in the Canton of Geneva (below).

disappeared locally in the Swiss Plateau with the intensification of agriculture (loss of traditionally managed semidry meadows (*Mesobromion*), elimination of hedges and other ligneous structures, replacement of meadows by pastures) and the strict separation between forests and agricultural land (loss of open wood and ecotone habitats). A decline in all *Cicadetta* species probably took place after the abandonment of traditional land use and the expansion of settlements in Ticino. Both *Tibicina* species from the Valais have been eliminated locally by the expansion of vineyards (Pillet, 1993) and artificial irrigation. These two species are the most important to focus on in nature

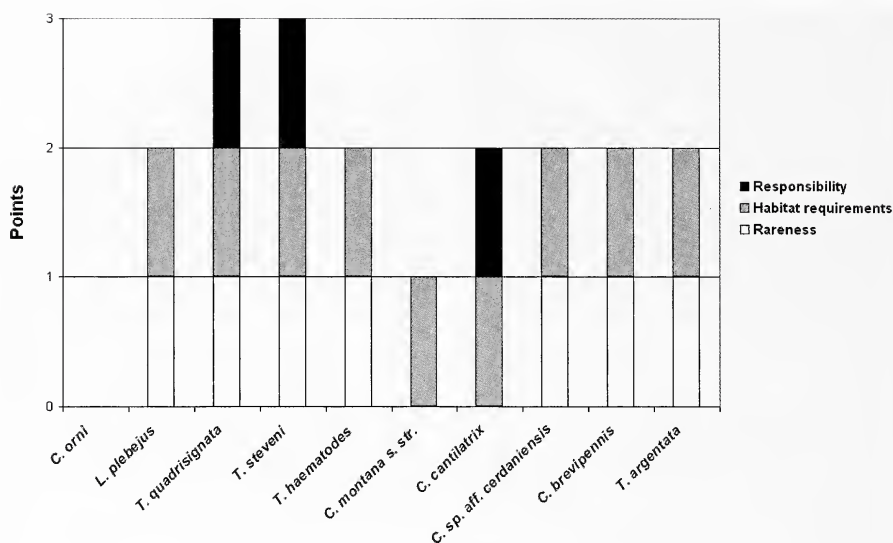


FIG. 15

Conservation issues estimated for each species in Switzerland: High national responsibility for the conservation of the species, critical habitat requirements and rareness (less than 20 grid cells occupied).

conservation programs because of their spatial isolation, their small distribution areas and their low densities. Overall, the most important conservation measure is to stop the habitat loss in the Valais. *C. orni*, *L. plebejus*, *T. haematodes* and *T. argentata* may extend their distribution area in the future supported by a milder climate.

Species of the *C. montana* complex can be assisted on sites with a warm and dry microclimate by thinning out forests on poor soil and by improving the structure of forest edges near dry and semidry meadows (Hertach, 2007). For example, well-adapted measures have been conducted in the Jura Mountains and in the Canton of Geneva within the last decades. We hope that the detailed knowledge on this insect group in combination with the planned Red List and the list of priority species will lead to more concrete conservation measures and an increasing political importance of these flagship species. The references found in non-scientific articles, and the remarkable media coverage given to solitary calling males of *C. orni* or *L. plebejus* underline the popularity of this insect group in Switzerland.

The gathered knowledge is an excellent base for additional field-work. Gaps in the dataset can be found in the central Jura Mountains and in the northern Prealps. It is likely that no additional species will be found, because of climatic and biogeographic patterns. The completeness of the inventory work is important for an assessment of the threat according to the criteria established in the IUCN. Furthermore, it forms the baseline to refine conservation strategies from the local to the national scale. Detailed field-work has to be redone in the central Valais in order to provide more accurate data on the overlapping distribution areas of the two *Tibicina* species. Furthermore, sites with old references or vouchers of *C. montana* s. l. should be visited again to get an impression on the long term development and threat of the populations.

ACKNOWLEDGEMENT

The Swiss cicada project is supported financially by a large number of donors: Wolfermann-Nägeli-Stiftung, Zigerli-Hegi-Stiftung, Walter Haefner Stiftung, Paul Schiller Stiftung, Biedermann-Mantel-Stiftung, Temperatio-Stiftung, Otto-Gamma-Stiftung, Fondo Guido Cotti and Stiftung Dr. Joachim de Giacomini; Pro Natura, Pro Natura Ticino, Pro Natura Graubünden, Pro Natura Vaud, Pro Natura Baselland and Pro Natura Basel-Stadt; Cantons of Geneva, Graubünden, Aargau, Basel-Land, Solothurn and Basel-Stadt; Museo Cantonale di Storia Naturale Lugano and the Swiss Central Fauna Data Bank (CSCF, Neuchâtel).

Many persons have provided their personal knowledge on observations or/and their collections. We are especially thankful to Paul Marchesi, Laurent Juillerat, André Rey, Christian Monnerat, Christian und Elodie Keim, Simon Pillet, Georg Artmann, Bruno Keist, Richard Vernier, Gottlieb Dandliker, Tomi Trilar, Stève Breitenmoser, Christophe Praz, Antoine Sierro, Yannick Chittaro, Bernard Bal, Regina Jöhl, Sibille Jenni Hertach, François Burnier, John Hollier, Eveline Currat, Martin Blattner, Christine Alexander, Ariane Bertaudon, Hélio Barros, Simon Birrer, Katarina Prosenc, Michel Beaud, Olivier Delapierre and François Cordillot. The curators of the Natural Museums in Geneva, Bern, Lausanne, Neuchâtel, Chur, Basel, Lucerne, Solothurn, Frauenfeld, Winterthur, Aarau, Sion, Schaffhausen, Lugano, Fribourg, Olten, St. Gallen, Liestal, Vienna, Paris and Ljubljana and of the collections of the Swiss Federal Institute of Technology Zurich and the Agroscope Changins Nyon assisted the visits, allowed to borrow voucher specimens or provided information. Michel Boulard, Masami Hayashi and Hans Duffels determined the *Platypleura* voucher. Natalie Danzi, Chiara Pradella, Lucia Pollini Paltrinieri, Roland Mühlethaler and Wolfgang Schedl organized literature references. Beatrice Wyss translated a Latin text from the 17th century, Simon Loader substantially improved the English of the manuscript, and two anonymous reviewers and the subject editor contributed valuable suggestions. Finally we are very grateful to Matija Gogala, Yves Gonseth and Daniel Burckhardt for the general advices in the planning and methods of this project.

REFERENCES

- ARTMANN, G. 1987. Die fremdsprachige Bergzikade (*Cicadetta montana peregrina*). *Mitteilungen der Entomologischen Gesellschaft Basel* 37(4): 190-192.
- BARBEY, P. 2010. Un événement pas si inhabituel que ça! A propos de l'article intitulé «Une cigale chante en ville de Lausanne». *24heures (newspaper; online)*, issue of 13 August 2010. Available from: <http://www.24heures.ch> (accessed 23 August 2010).
- BETTELINI, A. 1919. Discorso inaugurale del Congresso. *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft* 100(2): 3-14.
- BIEDERMANN, R. & NIEDRINGHAUS, R. 2004. Die Zikaden Deutschlands - Bestimmungstabellen für alle Arten. *Fründ, Scheessel*, 409 pp.
- BILLE, R. P. 1980. Le Bois de Finges et son Rhône. L'une des plus belles pinèdes d'Europe. *Edition W. Schoechli, Sierre*, 96 pp.
- BILLE, R. P. 1982. Les cigales de Romandie. *Diana* 99: 327-328.
- BILLE, R. P. & WERNER, P. 1986. Natur entdecken im Pfywald. *Verlag des Schweizerischen Vereins für Handarbeit und Schulreform, Liestal*, 144 pp.
- BOULARD, M. 1981. Matériaux pour une révision de la faune cicadéenne de l'Ouest paléarctique. *Bulletin de la Société Entomologique de France* 86: 41-53.

- BOULARD, M. 1995. Postures de cymbalisation, cymbalisations et cartes d'identité acoustique des cigales. Généralités et espèces méditerranéennes (Homoptera, Cicadoidea). *Ecole pratique des hautes Etudes, Biologie et Evolution des Insectes* 7/8: 1-72.
- BREMI, H. 1849. Uebersicht der schweizerischen Rhynchoten. *Mittheilungen der Naturforschenden Gesellschaft in Zürich* 34: 325-339.
- BUGNION, E. 1890. Introduction à la faune entomologique du Valais (pp. IX-XLIV). In: FAVRE, E. Faune des Coléoptères du Valais et des régions limitrophes. *Neue Denkschriften der allgemeinen schweizerischen Gesellschaft für die gesamten Naturwissenschaften, Druck Zürcher und Furrer, Zürich*, Band 31, XLIV + 448 pp.
- CARLINI, A. DE 1887. Rincoti del Sottoceneri. *Bullettino de la Società Entomologica Italiana, Firenze* 19: 258-277.
- CURTI, G. 1846. Storia naturale disposta con ordine scientifico e adattata alla comune intelligenza. *Tipografia Meyer, Lucerna*, 528 pp.
- DELARZE, R. 1987. L'origine des pelouses steppiques valaisannes à la lumière de leurs liens de parenté avec les régions limitrophes. *Bulletin de la Murithienne* 105: 41-70.
- DELARZE, R. 1988. Die Follatères Naturgetreu. Die Reichtümer der Natur im Wallis. *Departement für Umwelt des Kantons Wallis. Editions Pillet, Martigny*, 63 pp.
- DELARZE, R. & GONSETH, Y. 2008. Lebensräume der Schweiz: Ökologie – Gefährdung – Kennarten. *Hep Verlag AG, Bern*, 2. Auflage, 424 pp.
- DELLA BEFFA, G. 1925. Contributo alla conoscenza della fauna entomologica del Piemonte: Omotteri (Emitteri). *Bollettino della Società Entomologica Italiana* 57: 141-147.
- DIETRICH, K. 1872. Beiträge zur Kenntniss der im Kanton Zürich heimischen Insekten. *Entomologische Blätter aus der Schweiz* 2: 1-32.
- DÖDERLEIN, L. 1913. Beobachtungen über elsässische Tiere. *Mitteilungen der Philomathischen Gesellschaft in Elsass-Lothringen, Strassbourg* 5(1): 163-174.
- DORDA, D. 2012. Die Tierwelt im Saarland – eine Auswahl typischer Arten. *Saarland-Hefte* 5, 127 pp.
- DUCRET, J. 2010. Une cigale chante en ville de Lausanne. *24heures (newspaper, online)*, issue of 26 July 2010. Available from: <http://www.24heures.ch> (accessed 23 August 2010).
- DUFFELS, J. P. & VAN DER LAAN, P. A. 1985. Catalogue of the Cicadoidea (Homoptera, Auchenorrhyncha) 1956 – 1980. *Series entomologica, Dr. W. Junk Publishers, Dordrecht, Boston, Lancaster*, 414 pp.
- EITSCHBERGER, U. 1972. Zur Verbreitung von *Cicadetta montana* und *Tibicen haematodes* in Mainfranken (Hom., Cicadidae). *Entomologische Zeitschrift, Frankfurt* 82(18): 210-213.
- FARQUET, P. 1940. Le Mont Ravoire s/Martigny. *Bulletin de la Murithienne* 57: 34-89.
- FERRARI, P. M. 1892. Res Ligusticae XIX. Elenco dei Rincoti Ligustici (Emitteri e Cicadarii) fin'ora osservati. *Annali del Museo Civico di Storia Naturale di Genova Serie 2, Vol. XII*: 549-576.
- FIEBER, F.-X. 1876. Les Cicadines d'Europe d'après les originaux et les publications les plus récentes. Deuxième partie: Descriptions des espèces. *Revue et Magasin de Zoologie pure et appliquée* 4: 11-268.
- FISCHER, L. H. 1847. Ueber Sing-Cicaden. *Stettiner entomologische Zeitung* 8: 237-243.
- FUESSLIN, J. C. 1775. Verzeichnis der ihm bekannten Schweitzerischen Insekten. *Bey dem Verfasser und in Commission bey Heinrich Steiner und Compagnie, Zürich und Winterthur*, XII + 62 pp.
- GEISENHEYNER, L. 1887. Nicht eine, sondern zwei Singzikaden in der Rheinprovinz. *Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande, Westfalens und des Reg.-Bezirktes Osnabrück* 44: 116-117.
- GOGALA, M. 2002. Gesänge der Singzikaden aus Südost- und Mittel-Europa. *Denisia* 04: 241-248.
- GOGALA, M. 2012 (eds). Songs of European singing cicadas. Available from: www.cicadasong.eu (accessed 07 June 2012).

- GOGALA, M. & GOGALA, A. 1999. A checklist and provisional atlas of the Cicadoidea fauna of Slovenia (Homoptera: Auchenorrhyncha). *Acta entomologica slovenica* 7(2): 119-128.
- GOGALA, M. & TRILAR, T. 2004. Bioacoustic investigations and taxonomic considerations on the *Cicadetta montana* species complex (Homoptera: Cicadoidea: Tibicinidae). *Anais da Academia Brasileira de Ciências* 76(2): 316-324.
- GOGALA, M., TRILAR, T. & DROSOPOULOS, S. 2011. Two new species and a new genus of Cicadettini (Hemiptera, Cicadidae) from the Greek island of Evia. *Deutsche Entomologische Zeitschrift* 58(1): 105-117.
- GOGALA, M., TRILAR, T. & KRPAČ, V. T. 2005. Fauna of singing Cicadas (Auchenorrhyncha: Cicadoidea) of Macedonia – a bioacoustic survey. *Acta entomologica slovenica* 13(2): 103-126.
- GRIFFINI, A. 1896. Notes sur la faune entomologique piémontaise. X. Cicadidae, Membracidae et Scaridae. *Miscellanea Entomologica. Revue Entomologique Internationale* 4(11-12): 143-144.
- GROSJEAN, A. 2008. Une cigale a pris ses quartiers à Plainpalais. *Tribune de Genève (newspaper)*, issue of 31 July/1 August 2008.
- GÜNTHART, H. 1987. Zikaden (Auchenorrhyncha) (pp. D203-D299). In: *Ökologische Untersuchungen im Unterengadin, Bündner Natur-Museum Chur*, Band 12, 538 pp.
- GÜNTHART, H. & MÜHLETHALER, R. 2002. Provisorische Checkliste der Zikaden der Schweiz (Insecta: Hemiptera, Auchenorrhyncha). *Denisia* 04: 329-338.
- HAGEN, H. 1855. Die Sing-Cicaden Europa's. *Stettiner entomologische Zeitung* 16: 340-358.
- HAGEN, H. 1856a. Die Sing-Cicaden Europa's. *Stettiner entomologische Zeitung* 17: 27-37.
- HAGEN, H. 1856b. Die Sing-Cicaden Europa's. *Stettiner entomologische Zeitung* 17: 66-91.
- HALLER, A. VON 1765. Kurzer Auszug einer Beschreibung der Salzwerke in dem Amte Aelen. *Gedruckt bey Dan. Brunner und Albr. Haller Bern*, 170 pp.
- HAUPT, H. 1935. 2. Unterordnung: Gleichfüßler, Homoptera (pp. 115-262). In: BROHMER, P., EHLMANN, P. & ULMER, G. (eds). Die Tierwelt Mitteleuropas, *Quelle & Meyer, Leipzig*, Band IV, Insekten I. Teil, 288 pp.
- HAYASHI, M. & SAISHO, Y. 2011. The Cicadidae of Japan. *Seibundo-shinkosha, Tokyo*, 224 pp.
- HEER, O. & BLUMER, J. J. 1846. Der Kanton Glarus, historisch-geographisch-statistisch geschildert von den älteren Zeiten bis auf die Gegenwart. *Huber und Compagnie, St. Gallen und Bern*, XIV + 665 pp.
- HEGG, O., BÉGUIN, C. & ZOLLER, H. 1993. Atlas schutzwürdiger Vegetationstypen der Schweiz. *Bundesamt für Umwelt, Wald und Landschaft, Bern*, 160 pp.
- HERTACH, T. 2004. Beitrag zur Klärung des Artkomplexes *Cicadetta montana* – Bergzikade (Hemiptera, Cicadidae): Entdeckung einer Singzikadenart mit ungewissem taxonomischem Status in der Nordschweiz. *Mitteilungen der Entomologischen Gesellschaft Basel* 54(2): 58-66.
- HERTACH, T. 2007. Three species instead of only one: Distribution and ecology of the *Cicadetta montana* species complex (Hemiptera: Cicadoidea) in Switzerland. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 80: 37-61.
- HERTACH, T. 2008. A new cicada species for Switzerland: *Tettigetia argentata* (Olivier, 1790) (Hemiptera: Cicadoidea). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 81: 209-214.
- HERTACH, T. 2010. Pechader-Bergzikade (*Cicadetta montana*) (p. 183). In: INEICHEN, S. & RUCKSTUHL, M. (eds). Stadtf fauna – 600 Tierarten der Stadt Zürich. *Haupt Verlag Bern, Stuttgart, Wien*, 446 pp.
- HERTACH, T. 2011. Spectacular song pattern from the Sicilian Mountains: The new cicada species *Cicadetta anapaistica* sp. n. (Hemiptera: Cicadidae). *Zootaxa* 2771: 25-40.
- HERTACH, T. & POLLINI PALTRINIERI, L. 2012. Le cicale (Hemiptera: Cicadidae) del Cantone Ticino (Svizzera). *Bollettino della Società ticinese di scienze naturali* 100: 43-51.
- HOCH, H. 2011. Fauna Europaea: Cicadidae and Tibicinidae. *Fauna Europaea Version 2.4*, Available from: www.faunaeur.org (accessed 07 June 2012).

- HOFMÄNNER, B. 1924. Die Hemipterenfauna des Schweizerischen Nationalparks (Heteroptera und Cicadinen). *Denkschrift der Schweizerischen Naturforschenden Gesellschaft* 60: 1-88.
- HOLLIER, J. 2012. Ordre Auchenorrhyncha (pp. 59-62). In: MERZ, B. (eds). Liste annotée des insectes (Insecta) du canton de Genève. *Instrumenta Biodiversitatis (Geneva)* 8, 532 pp.
- HOLZINGER, W. E., KAMMERLANDER, I. & NICKEL, H. 2003. The Auchenorrhyncha of Central Europe. Volume 1: Fulgoromorpha, Cicadomorpha excl. Cicadellidae. *Brill Academic Publishers, Leiden*, 673 pp.
- HUBER, A. 1916. Die wärmeliebende Tierwelt der weitem Umgebung Basels. *Archiv für Naturgeschichte, Berlin, Abteilung A* 82(7): 1-120.
- HÜEBNER, T. 1904. Systematisches Verzeichnis der deutschen Zikadinen. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 60: 253-277.
- HUGEL, S., MATT, F., CALLOT, H., FELDTRAUER, J. & BRUA, C. 2008. Présence de *Cicadetta brevipennis* Fieber, 1876 en Alsace (Hemiptera, Cicadidae). *Bulletin de la Société Entomologique de Mulhouse*, 64(1): 5-10.
- JACOBS, W. & RENNER, M. 1988. Biologie und Ökologie der Insekten. *Gustav Fischer Verlag, Stuttgart*, 2. Auflage, 609 pp.
- KEIM, C. 1999. Les cigales musiciennes accomplies. *Diana, Chasse/Nature* 12: 13-15.
- KUNTZE, R. 1931. Vergleichende Beobachtungen und Betrachtungen über die xerotherme Fauna in Podolien, Brandenburg, Österreich und der Schweiz. *Zeitschrift für Morphologie und Ökologie der Tiere* 21: 629-690.
- KUNZ, V., NICKEL, H. & NIEDRINGHAUS, R. 2011. Fotoatlas der Zikaden Deutschlands - Photographic Atlas of the Planthoppers and Leafhoppers of Germany. *Fründ, Scheessel*, 293 pp.
- LABRAM, J. D. & IMHOFF, L. 1845. Insekten der Schweiz. Die vorzüglichsten Gattungen je durch eine Art bildlich dargestellt. *Dahnmaier's Buchhandlung, Basel*, Viertes Bändchen, Hefte 61-81.
- MARCHESI, P., SIERRO, A. & FOURNIER, J. 2002. Chronique entomologique valaisanne pour 2001 et 2002. *Bulletin de la Murithienne* 120: 25-32.
- MEINEKE, T. 2012. Bergsingzikaden *Cicadetta cantilatrix* Sueur & Puissant, 2007, *Cicadetta brevipennis* Fieber, 1876 und *Cicadetta montana* s. str. (Scopoli, 1772) im mittleren Deutschland (Auchenorrhyncha, Cicadidae, Cicadettinae). *Entomologische Nachrichten und Berichte* 56(2): 133-142.
- MELICHAR, L. 1896. Cicadinen (Hemiptera-Homoptera) von Mittel-Europa. *Felix L. Dames, Berlin*, 364 pp.
- METCALF, Z. P. 1963. General Catalogue of the Homoptera, Fascicle VIII, Cicadoidea. Part 1: Cicadidae, Section 1 Tibicinidae. *University of North Carolina State College, Raleigh*, 585 pp.
- MEYER-DÜR, R. 1860. Ein Blick über die schweizerische Orthoptern-Fauna. *Neue Denkschriften der Allgemeinen schweizerischen Gesellschaft für die gesammten Naturwissenschaften, Zürich*, Band 17, 32 pp.
- MILDE, J. 1865. Zoologische Mitteilungen aus Meran. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 15: 961-962.
- MILDE, J. 1866. Naturgeschichtliche Mittheilungen über Meran. Erste Mittheilung: Die Sing-Cicaden. *Realschule zum heiligen Geist, Breslau*, 49 pp.
- MOFFET, T., WOTTON, E., GESNER, K. & PENNY, T. 1634. Insectorum sive minimorum animalium theatrum. *Ex officinâ typographicâ Thomas Cotes, London*, 326 pp.
- MOULDS, M. 2005. An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. *Records of the Australian Museum* 57: 375-446.
- MÜLLER, P. 1969. *Cicadetta montana* Scop. (Homoptera-Cicadidae) im Saarland. *Faunistisch-floristische Notizen aus dem Saarland* 2(3): 24-25.
- MUHIEDDINE, F. 2004. Une cigale chante à la Tour-de-Peilz. *24heures (newspaper)*, issue of 17 August 2004.

- MUSÉE D'HISTOIRE NATURELLE FRIBOURG, NATURHISTORISCHES MUSEUM FREIBURG 2004. Rapport d'activité – Jahresbericht 2003, 83 pp.
- NAST, J. 1972. Palearctic Auchenorrhyncha (Homoptera). An annotated check list. *Polish scientific publishers, Warszawa*, 550 pp.
- NAST, J. 1987. The Auchenorrhyncha (Homoptera) of Europe. *Annales Zoologici Warszawa* 40(15): 355-661.
- NICKEL, H. 2003. The leafhoppers and planthoppers of Germany (Hemiptera, Auchenorrhyncha): patterns and strategies in a highly diverse group of phytophagous insects. *Pensoft, Sofia and Moscow*, 460 pp.
- NICKEL, H. & REMANE, R. 2003. Verzeichnis der Zikaden (Auchenorrhyncha) der Bundesländer Deutschlands. In: KLAUSNITZER, B. (eds). Entomofauna Germanica 6. *Entomologische Nachrichten und Berichte*, Beiheft 8, 344 pp.
- NIEHUIS, M. & SIMON, L. 1994. Zum Vorkommen der Blutaderzikade – *Tibicina haematodes* (Scop.) – und Bergzikade – *Cicadetta montana* (Scop.) – in Rheinland-Pfalz (Homoptera: Cicadidae). *Fauna Flora Rheinland Pfalz* 7(2): 253-264.
- NIKOLIC, D. 2010. La cigale est de retour à Plainpalais. *Tribune de Genève (newspaper, online)*, issue of 28 June 2010. Available from: <http://www.tdg.ch> (accessed 29 June 2010).
- OGGIER, P.-A. 1995. Erkenne die Natur im Wallis – die Fauna. *Edition Pillet, Martigny*, Deutsche Ausgabe, 279 pp.
- OSHANIN, B. 1912. Katalog der paläarktischen Hemipteren (Heteroptera, Homoptera-Auchenorrhyncha und Psylloidea). *Friedländer & Sohn, Berlin*, 187 pp.
- PAVESI, P. 1873. Materiali per una fauna del cantone Ticino. *Atti della Società Italiana di Scienze Naturali, Milano* Vol XVI. Fasc. I., 33 pp.
- PERTY, M. 1879. Erinnerungen aus dem Leben eines Natur- und Seelenforschers des neunzehnten Jahrhunderts. *C. F. Winter'sche Verlagshandlung, Leipzig und Heidelberg*, 486 pp.
- PILLET, J.-M. 1993. Les Cigales du Valais. *Bulletin de la Murithienne* 111: 95-113.
- POPOV, A., BEGANOVIĆ, A. & GOGALA, M. 1997. Bioacoustics of singing cicadas on the western palaearctic: *Tettigetta brullei* (Fieber 1876) (Cicadoidea: Tibicinidae). *Acta entomologica slovenica* 5: 89-101.
- PUISSANT, S. 2006. Contribution à la connaissance des cigales de France: Géonémie et écologie des populations (Hemiptera, Cicadidae). *Association pour la Caractérisation et l'Etude des Entomocénoses, Bédailhac et Aynat*, 193 pp.
- PUISSANT, S. & BOULARD, M. 2000. *Cicadetta cerdaniensis*, espèce jumelle de *Cicadetta montana* décryptée par l'acoustique (Auchenorrhyncha, Cicadidae, Tibicinidae). *Ecole pratique des hautes Etudes, Biologie et Evolution des Insectes* 13: 111-117.
- PUISSANT, S. & SUEUR, J. 2010. A hotspot for Mediterranean cicadas (Insecta: Hemiptera: Cicadidae): new genera, species and songs from southern Spain. *Systematics and Biodiversity* 8(4): 555-574.
- PUISSANT, S. & SUEUR, J. 2011. *Dimissalna*, a cicada genus that remained unnoticed in France (Insecta: Hemiptera: Cicadidae). *Annales de la Société entomologique de France* 47(3-4): 519-523.
- PUTON, A. 1899. Catalogue des Hémiptères (Hétéroptères, Cicadines et Psyllides) de la faune Paléarctique. Quatrième édition. *Société française d'entomologie, Caen*, 121 pp.
- RADIO TÉLÉVISION SUISSE ROMANDE (RTSR) 2010. Le Journal. Broadcasted on 16 July 2010.
- REMANE, R. & WACHMANN, E. 1993. Zikaden kennenlernen – beobachten. *Naturbuch Verlag, Augsburg*, 288 pp.
- ROBERT, P.-A. 1937. Les Insectes: Hyménoptères, Lépidoptères, Rhynchotes, Diptères. *Editions Delachaux & Niestlé S.A., Neuchâtel et Paris*, Volume 2, 270 pp.
- ROUGEMONT, P. DE 1880. Note sur l'helicopsyche sperata. *Bulletin de la Société des Sciences Naturelles de Neuchâtel* 12: 29-38.
- SAUSSURE, H.-B. DE 1780. Voyages dans les Alpes, précédés d'un Essai sur l'Histoire Naturelle des Environs de Genève. *Samuel Fauche, Imprimeur & Libraire du Roi, Neuchâtel*, Tome Premier, 540 pp.

- SCHEDL, W. 1973. Zur Verbreitung, Bionomie und Ökologie der Singzikaden (Homoptera: Auchenorrhyncha, Cicadidae) der Ostalpen und ihrer benachbarten Gebiete. *Berichte des naturwissenschaftlich-medizinischen Vereins Innsbruck* 60: 79-94.
- SCHEDL, W. 2000. Taxonomie, Biologie und Verbreitung der Singzikaden Mitteleuropas (Insecta: Homoptera: Cicadidae et Tibicinidae). *Berichte des naturwissenschaftlich-medizinischen Vereins Innsbruck* 87: 257-271.
- SCHEDL, W. 2002. Die Verbreitung der fünf Singzikaden-Arten in Österreich (Hemiptera: Cicadoidea). *Denisia* 04: 231-239.
- SCHEDL, W. 2004. Die Singzikaden des Burgenlands (Österreich) (Insecta: Homoptera, Cicadoidea). *Linzer Biologische Beiträge* 36: 913-917.
- SCHERDLIN, P. 1910. Eine für die deutsche Fauna neue grosse Cicade, *Cicada plebeja* Scop. *Annales de la Société entomologique de Belgique* 54: 142-143.
- SCHNETZLER, J.-B. 1877. Discours d'ouverture de la 60e session de la Société Helvétique des Sciences Naturelles à Bex. *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft* 60: 3-30.
- SCHWOERBEL, W. 1957. Die Wanzen und Zikaden des Spitzberges bei Tübingen, eine faunistisch-ökologische Untersuchung (Hemipteroidea: Heteroptera und Cicadina = Homoptera Auchenorrhyncha). *Zeitschrift für Morphologie und Ökologie der Tiere, Berlin* 45: 462-560.
- SEGANTINI, G. 1937. La Bregaglia. *Quaderni grigionitaliani* 6(1): 3-17.
- SEILER, A. 1847. Uebersicht der im Canton Schaffhausen vorkommenden Thiere. *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft* 32: 160-175.
- SERVADEI, A. 1967. Fauna d'Italia. Rhynchota (Heteroptera, Homoptera, Auchenorrhyncha). Catalogo topografico e sinonimico. *Edizione Calderini, Bologna*, 851 pp.
- SIEBOLD, C. T. VON 1847. Ueber die Verbreitung der singenden Cicaden in Deutschland. *Stettiner entomologische Zeitung* 8: 6-18.
- SIERRO, A. & KEIM, C. 1999. Activité entomologique valaisanne pour 1997 et 1998. *Bulletin de la Murithienne* 117: 61-71.
- SIERRO, A., KEIM, C. & MARCHESI, P. 2000. Activité entomologique valaisanne pour 1999 et 2000. *Bulletin de la Murithienne* 118: 93-103.
- STABILE, A. G. & STABILE, F. 1856. Degli Insetti del Cantone Ticino. *L'educatore della Svizzera italiana* Anno 1: 230-240.
- STOLL, O. 1901. Über xerotherme Relikte in der Schweizer Fauna der Wirbellosen. *Jahresberichte der Geographisch-Ethnographischen Gesellschaft in Zürich* 2: 145-208.
- SUEUR, J. & AUBIN, T. 2003. Specificity of cicada calling songs in the genus *Tibicina* (Hemiptera, Cicadidae). *Systematic Entomology* 28: 481-492.
- SUEUR, J. & PUISSANT, S. 2007a. Similar look but different song: a new *Cicadetta* species in the *montana* complex (Insecta, Hemiptera, Cicadidae). *Zootaxa* 1442: 55-68.
- SUEUR, J. & PUISSANT, S. 2007b. Biodiversity eavesdropping: bioacoustics confirms the presence of *Cicadetta montana* (Insecta: Hemiptera: Cicadidae) in France. *Annales de la Société entomologique de France* 43(1): 126-128.
- SUEUR, J., PUISSANT, S. & PILLET, J.-M. 2003. An Eastern mediterranean cicada in the West: first record of *Tibicina steveni* (Krynicky, 1837) in Switzerland and France (Hemiptera, Cicadidae). *Revue française d'Entomologie* 25: 105-111.
- SUEUR, J., PUISSANT, S., SIMÕES, P. S., SEABRA, S., BOULARD, M. & QUARTAU, J. A. 2004. Cicadas from Portugal: revised list of species with eco-ethological data (Hemiptera: Cicadidae). *Insect Systematics and Evolution* 35: 177-187.
- SULZER, J. H. 1761. Die Kennzeichen der Insekten. *Steiner'sche Buchhandlung, Zürich und Winterthur*, XXVIII + 203 pp.
- TRILAR, T., GOGALA, M. & SZWEDO, J. 2006. Pyrenean Mountain Cicada *Cicadetta cerdaniensis* Puissant & Boulard (Hemiptera: Cicadomorpha: Cicadidae) found in Poland. *Polskie Pismo Entomologiczne* 75(2): 313-320.

- TRILAR, T. & HERTACH, T. 2008. Three species of Mountain Cicadas *Cicadetta montana* (sensu lato) found in northern Italy. *Bulletin of Insectology* 61(1): 185-186.
- TRILAR, T. & HOLZINGER, W. E. 2004. Bioakustische Nachweise von drei Arten des *Cicadetta montana*-Komplexes aus Österreich (Insecta: Hemiptera: Cicadoidea). *Linzer biologische Beiträge* 36(2): 1383-1386.
- TSCHUDI, F. VON 1872. Das Thierleben der Alpenwelt. Naturansichten und Thierzeichnungen aus dem schweizerischen Gebirge. *Verlagsbuchhandlung J. J. Weber, Leipzig*, neunte, vielfach vermehrte und verbesserte Auflage, XV + 593 pp.
- VERNIER, R. 1996. Un chanteur isolé de *Lyristes plebejus* (Scop.) (Hemiptera, Cicadidae) à l'Allondon. *Bulletin romand d'entomologie* 14: 147-152.
- VOGEL, R. 1935. Die blutrote Singzikade (*Tibicen haematodes* Scop.) in Württemberg und Deutschland. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 91: 146-154.
- VOGEL, R. 1937. Weiteres über Verbreitung und Lebensweise der Blutroten Singzikade (*Tibicen haematodes* Scop.). *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 93: 116-123.
- VON SALIS, C. U. 1807. Fragmente zur Entomologie der Alpen. *Alpina - eine Zeitschrift der genauern Kenntnis der Alpen gewidmet, Winterthur* 2: 64-104.
- WAGNER, W. & FRANZ, H. 1961. Auchenorrhyncha (Zikaden) (pp. 74-158). In: FRANZ, H. Die Nordostalpen im Spiegel ihrer Landtierwelt. *Universitätsverlag Wagner Innsbruck*, Band 2, 792 pp.
- ZSCHOKKE, F. 1928. Die Tierwelt des Kantons Tessin. Ein Beitrag zur Kenntnis der Südschweiz. *Frobenius Verlag, Basel*, 145 pp.

On the genera *Acanthobythus* Normand, 1930 and *Ceratobythus* Normand, 1932 (Coleoptera: Staphylinidae: Pselaphinae)

Claude BESUCHET¹, Giulio CUCCODORO² & Giorgio SABELLA³

¹ Muséum d'histoire naturelle, Case postale 6434, CH-1211 Genève 6, Switzerland.

E-mail: betty.ott@bluewin.ch

² Muséum d'histoire naturelle, Case postale 6434, CH-1211 Genève 6, Switzerland.

E-mail: giulio.cuccodoro@ville-ge.ch (corresponding author)

³ Dipartimento di Scienze Biologiche, Geologiche ed Ambientali dell'Università - sezione Biologia Animale - via Androne 81, I - 95124 Catania.

E-mail: sabellag@unict.it

On the genera *Acanthobythus* Normand, 1930 and *Ceratobythus* Normand, 1932 (Coleoptera: Staphylinidae: Pselaphinae) - The types species of the monotypic North Algerian Bythinines genera *Acanthobythus* Normand, 1930 and *Ceratobythus* Normand, 1932 are revised, with their aedeagi illustrated for the first time. The lectotype of *Bythoxenus* (*Acanthobythus*) *araneipes* Normand, 1930 is designated. These two genera are synonyms with *Tychobythinus* Ganglbauer, 1896 (*Acanthobythus* Normand, 1930 and *Ceratobythus* Normand, 1932 **syn. nov.**), and the type species of the latter is consequently recombined *Tychobythinus monoceros* (Normand, 1932) **comb. nov.**

Keywords: Taxonomy - Bythinini - Algeria - *Ceratobythus* - *Acanthobythus* - *Tychobythinus*.

INTRODUCTION

In the catalogues of Newton & Chandler (1989) and Löbl & Besuchet (2004), the pselaphine tribe Bythinini appears represented in North Africa only by the genera *Bryaxis* Kugelann, 1794, *Ceratobythus* Normand, 1932 and *Tychobythinus* Ganglbauer, 1896, with *Acanthobythus* Normand, 1930 listed as a synonym of *Tychobythinus* Ganglbauer, 1896. The latter synonymy (Newton & Chandler, 1989: 48; Löbl & Besuchet, 2004: 314) has however never been adequately argued.

In this study, we examined the types (and only material available so far) of the types species of the monotypic genera *Acanthobythus* and *Ceratobythus*, i.e. *A. araneipes* (Normand, 1930) and *C. monoceros* (Normand, 1932). These species are redescribed with their aedeagi illustrated for the first time. The lectotype of *A. araneipes* is designated. We reassess their taxonomic placement and consider both, *Acanthobythus* and *Ceratobythus*, as synonyms of *Tychobythinus*.

MATERIAL AND METHODS

The study is based on material loaned half a century ago from H. Normand directly to the first author; it will remain housed in MHNG.

The body length is measured from the anterior clypeal margin to the posterior margin of the last visible abdominal tergite. The length and width of body parts were measured in dorsal view between points of maximum extension, e.g. the head length is measured between the anterior clypeal margin and the posterior margin of the neck; the head width includes eyes, the elytral length is along the suture, and the elytral width is that of both elytra combined. The abdominal segments are numbered from the first visible segment onwards, i.e. from the 1st tergite (fourth morphological segment) and 1st sternite (third morphological segment). The terminology for the external morphology follows otherwise that proposed by Chandler (2001).

TAXONOMY

Tychobythinus Ganglbauer, 1896

Tychobythinus Ganglbauer, 1896: 170; type species: *Bythinus ottonis* Ganglbauer, 1896 (subsequent designation).

Acanthobythus Normand, 1930: 163; type species: *Bythoxenus araneipes* Normand, 1930 (monotypy).

Ceratobythus Normand, 1932: 15; type species: *Bythoxenus monoceros* Normand, 1932 (monotypy) **syn. nov.**

COMMENTS: Normand in 1930 and 1932, described respectively *Acanthobythus* and *Ceratobythus* as new subgenera of *Bythoxenus* Motschulsky, 1860. Jeannel (1956) raised *Acanthobythus* to genus rank, arguing that it was certainly a distinct lineage from both his *Anopsibythus* Jeannel, 1956 (erected to accommodate five anophthalmous Algerian species and presently a synonym of *Tychobythinus*) and *Ceratobythus*, and « also completely unrelated » to *Bythoxenus*.

In both, the World catalogue of the genera of Pselaphinae (Newton & Chandler, 1989) and Pselaphinae in the Catalogue of Palaearctic Coleoptera (Löbl & Besuchet, 2004), *Ceratobythus* is listed as a valid while *Acanthobythus* is a synonym of *Tychobythinus*. The latter placement has however never been discussed, neither *A. araneipes* explicitly transferred.

Acanthobythus and *Ceratobythus* share with the 89 species-rich Holarctic genus *Tychobythinus* the pronotal and elytral foveal systems, as well as most other external characters, such as the antennal scape much longer than wide, narrowed and flattened at basal third and widest at distal third, the maxillary palpi with segments II and III bearing many prominent tubercles and the apical segment distinctly longer than wide and widest at basal third, and prominent tubercles on the anterior margin of pro-trochanters and profemora. In fact *Acanthobythus* and *Ceratobythus* differ from each other and from members of *Tychobythinus* only by head features. The conformation of their aedeagi also fits within the variation observed in *Tychobythinus*. Therefore, we consider that there is no justification to maintain them as distinct genera.

Tychobythinus araneipes (Normand, 1930)

Figs 1-4

Bythoxenus (Acanthobythus) araneipes Normand, 1930: 163, figs 1 (habitus) and 2 (head, lateral view);

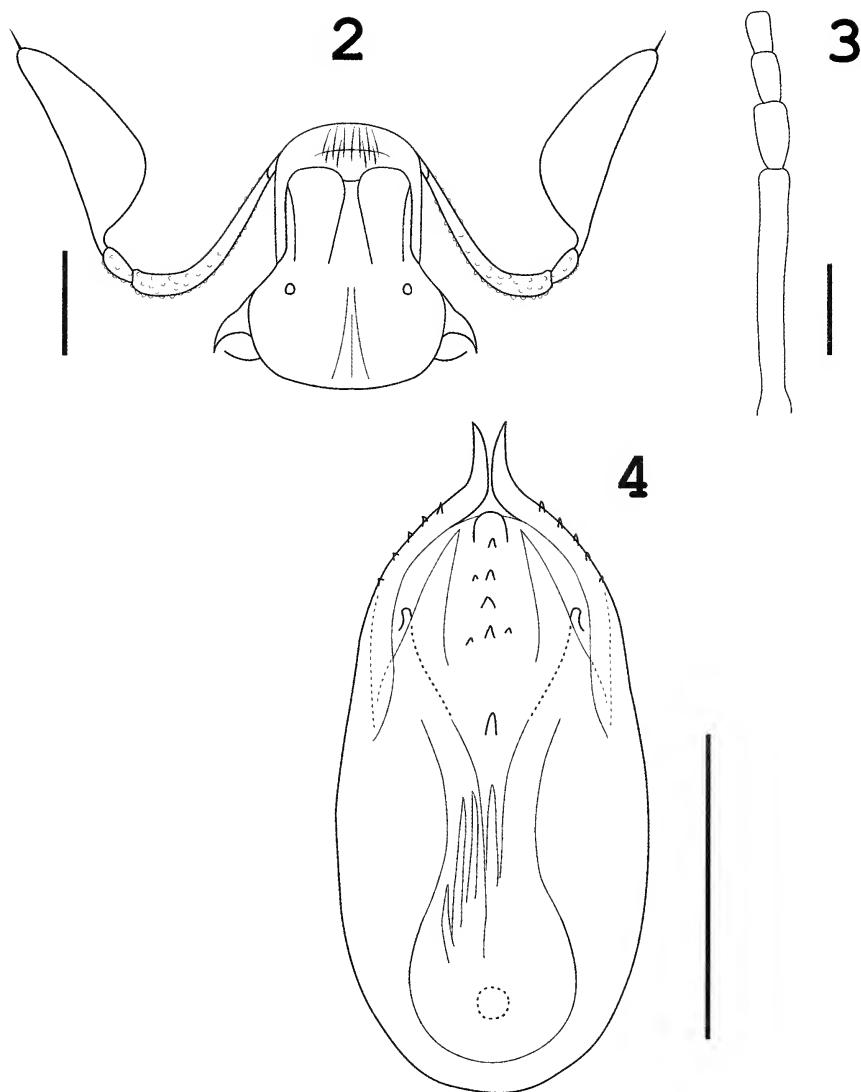
Acanthobythus araneipes. – Jeannel, 1956: 65, figs 59 (habitus) and 60 (maxillary palpus).

TYPE MATERIAL: Lectotype (present designation); Northeastern Algeria, Skikda province; male, Philippeville, route de Collo, X.1929 (H. Normand) (MHNG). Paralectotypes, 2 females, same data as lectotype (MHNG).



FIG. 1

Dorsal habitus of *Acanthobythus araneipes*, lectotype. Scale bar 1 mm.



FIGS 2-4

Acanthobythus araneipes, lectotype. (2) Head and maxillary palpi, dorsal view. (3) Base of antenna. (4) Aedeagus, dorsal view. Scale bar 0.1 mm.

REDESCRIPTION: Body (Fig. 1) 1.40-1.45 mm long, uniformly pale brown-reddish; wingless and anophthalmous. Pubescence fairly uniform, slightly longer on anterior portion of elytra and denser on pronotum, consisting of setae distant from each other by approximately their length, slightly arcuate and semi-erect to recumbent, predominantly about as long as apical width of metafemora (0.06 mm).

Head (Fig. 2) with frontal lobe moderately depressed medially. Tempora bearing each a conspicuous, acute spine (length 0.06-0.07 mm) obliquely oriented dorsally and slightly curved posteriorly, sharp clypeal ridge extended posteriorly to tip of each temporal spine. Occipital region slightly convex, with short medial occipital carina. Antennae (Fig. 3) 0.80 mm long with scapus more than 5 times as long (0.27 mm) as wide (0.05 mm), antennomere II oval (length 0.07 mm; width 0.04 mm). Maxillary palpi (Fig. 2) with segment I almost indistinct; II (length 0.22 mm; width 0.02-0.04 mm) distinctly curved on apical half and gradually enlarged until apical third, with posterior surface covered with tubercles distant from each other by slightly more than their diameter; III (0.07 mm/0.04 mm) fairly oval, bearing a few tubercles; IV (0.25 mm/0.09 mm) securiform and finely pubescent, its lateral margin slightly concave.

Pronotum wider (0.33 mm) than long (0.30 mm), almost spherical, narrower anteriorly than posteriorly with maximal width at anterior third; antebasal sulcus well-marked, joining lateral foveae. Disc covered in middle with shallow areolate punctation and laterally with tubercles separated from each other by 3-4 times their diameter.

Elytra wider (0.56 mm) than long (0.50 mm), more convex transversely than longitudinally; pair of deep basal elytral foveae, internal fovea joint to complete sutural stria and external fovea extended by rather wide and deep depression reaching elytral mid-length at most; subhumeral elytral fovea extended dorsally by short vertical carina and ventrally by entire lateral carina.

Metasternum with lateral mesocoxal and lateral metasternal foveae deep and tomentose.

Abdomen rather long (0.52 mm) with first tergite 0.15 mm long; each tergite with a pair of long discal setae.

Legs with trochanters simples; anterior edge of protrochanters with 3-4 small prominent tubercles; metatrochanters much longer than mesotrochanters. Profemora relatively robust (0.38 mm/0.09 mm) bearing on anterior margin row of 14 tubercles, first 4-5 more prominent than others; mesofemora (0.42 mm/0.07 mm) and meta-femora (0.51 mm/0.06 mm) more slender. Protibiae (0.39 mm/0.02-0.04 mm) and mesotibiae (0.40 mm/0.02-0.04 mm) straight; metatibiae (0.55 mm/0.02-0.05 mm) somewhat curved subapically. Metatarsi very thin (length I: 0.03 mm; II: 0.19 mm and III: 0.11 mm) with single claw (length 0.02 mm).

Male: Gular region behind labium with deep and broad depression margined posteriorly by conspicuous transversely compressed acute medial process projecting ventrally, latter medially sulcate and bearing two tufts of modified setae grouped at tip; gular region behind that process vertical, laterally with two deep longitudinal sulci bearing each a long semi-erect seta apically arcuate anteriorly. Aedeagus (Fig. 4), 0.22 mm long, with parameres apically acuminate and straight, each bearing with four small denticles on outer margin; internal sac with 7 thin and slender sclerites.

Female: Gular region behind labium shallowly depressed; posterior portion convex, with a medial ridge, and laterally with two shallow longitudinal sulci bearing each couple of long semi-erect setae apically arcuate anteriorly.

COMMENTS: *Tychobythinus araneipes* is the only member of the genus to possess conspicuous temporal spines.

The species is known only by the types, which were collected in October by soil washing at base of oaks and around roots of *Asphodelus* sp. The statement of Jeannel (1956) that the species was known only from female sex was erroneous.

In box 67 of the collection the "Afrique du Nord" in MNHN we found a mounting card bearing remnants of glue and with attached label "*Acantobythus araneipes* Philippeville X.1929 Normand"; these may have belonged to the second male and 4th type mentioned by Normand in the original description (probably examined by Jeannel).

***Tychobythinus monoceros* (Normand, 1932) comb. nov.**

Figs 5-7

Bythoxenus (*Ceratobythus*) *monoceros* Normand, 1932: 16, figs 2-3 (head dorsal and lateral view).

Ceratobythus monoceros. – Jeannel, 1956: 64, fig. 58 (habitus).

TYPE MATERIAL: Holotype, Northeastern Algeria, Bejaia province; male, Adekar (Soummam), X.1931 (H. Normand) (MHNG).

REDESCRIPTION: Body (Fig. 5) 1.50 mm long, uniformly pale brown-reddish; wingless and anophthalmous. Pubescence fairly uniform, slightly longer on anterior portion of elytra and denser on pronotum, consisting of setae distant from each other by slightly less than their length, slightly arcuate and semi-erect to recumbent, predominantly slightly longer than apical width of metafemora (0.06 mm); presence of several much longer setae on head, pronotum and elytra; each tergite with a pair of long discal setae.

Head (Fig. 6) with pair of 0.07 mm long longitudinally compressed antennal lobes extended each ventrally with short spine bearing 3 tufts of short setae; antennal lobes separated by conspicuous mediodorsal conical horn-like process (length 0.10 mm) obliquely projecting anterad and bearing at tip curved seta 0.42 mm long, (broken off the holotype by dissection). Frons deeply depressed, margined with sharp ridge almost to round tempora and bearing short additional medial process with two diverging tufts of aggregated setae. Occipital region slightly convex with long medial occipital carina reaching anterior edge of vertexal foveae. Tempora each with a long seta curved anterad. Antennae 0.80 mm long with scapus 5 times as long (0.25 mm) as wide (0.05 mm) and antennomere II oval (length 0.09 mm; width 0.05 mm wide). Maxillary palpi with segment I almost indistinct; II (length 0.22 mm; width 0.02-0.04 mm) somewhat curved and gradually enlarged from base to apex, with posterior surface covered with tubercles distant from each other by slightly more than their diameter; III (0.05 mm/0.04 mm) fairly oval bearing a few tubercles; IV (0.24 mm/0.07 mm) securiform and finely pubescent. Gular region rather broad, gently convex and bearing two minute tubercles.

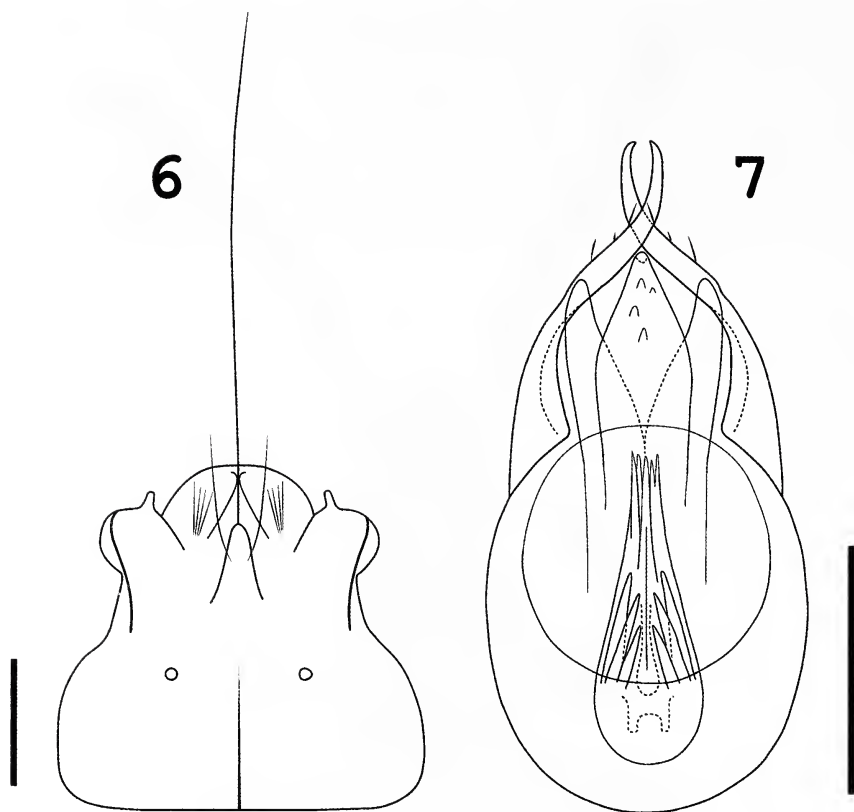
Pronotum wider (0.33 mm) than long (0.30 mm), almost spherical, narrower anteriorly than posteriorly, with maximal width slightly anterior middle; antebasal sulcus well-marked, joining lateral foveae. Disc almost smooth in middle and covered laterally with low tubercles separated from each other by 3-4 times their diameter.

Elytra wider (0.54 mm) than long (0.50 mm), more convex transversely than longitudinally; pair of deep basal elytral foveae, internal fovea joint to complete sutural stria, and external fovea extended by rather wide and deep depression reaching at most



FIG. 5

Dorsal habitus of *Ceratobypus monoceros*, holotype, frontal macroseta broken. Scale bar 1 mm.



FIGS 6-7

Ceratobythus monoceros, holotype. (6) Head, dorsal view. (7) Aedeagus, dorsal view. Scale bar 0.1 mm.

elytral mid-length; subhumeral elytral fovea extended dorsally by short vertical carina, ventrally by entire lateral carina.

Metasternum with lateral mesocoxal and lateral metasternal foveae deep and tomentose.

Abdomen rather short (0.45 mm).

Legs with trochanters simples; anterior edge of protrochanters with 3-4 small prominent tubercles; metatrochanters much longer than mesotrochanters. Profemora relatively robust (0.44 mm/0.10 mm), each bearing row of 8 small tubercles on basal third of anterior margin, first 3-4 much more prominent than others, larger than wide; mesofemora (0.45 mm/0.08 mm) and metafemora (0.51 mm/0.06 mm) more slender. Protibiae (0.40 mm/0.05 mm) and mesotibiae (0.40 mm/0.05 mm) straight; metatibiae (0.55 mm/0.05 mm) somewhat curved subapically.

Male: Aedeagus (Fig. 7), 0.27 mm long, with parameres slender in apical portion and inter-crossed subapically, without denticles on outer margin; internal sac with 11 thin and slender sclerites.

Female: Unknown.



FIGS 8-9

(8) Left lateral view of head and pronotum of *Acanthobythus araneipes*, lectotype. (9) *Ceratobythus monoceros*, holotype, frontal macroseta broken. Scale bar 0.5 mm.

COMMENTS: Within *Tychobythinus*, the presence of a conspicuous frontal horn is unique to *T. monoceros*.

Normand (1932) specified that he found only one specimen in a bag of clay soil at the foot of a bank. He observed that while moving, it was touching the soil with the antennae, while his long frontal sensory seta was apparently used to detect obstacles.

According to Jeannel (1956: 64) the holotype was a female.

REFERENCES

- CHANDLER, D. S. 2001. Biology, morphology, and systematics of the ant-like litter beetles of Australia (Coleoptera: Staphylinidae: Pselaphinae). *Memoirs on Entomology, International* 15: 1-560.
- GANGLBAUER, L. 1896. Ein neue *Bythinus* vom Neusiedler See. *Verhandlungen der Kaiserlich-Königlichen Zoologische-Botanischen Gesellschaft in Wien* 46: 170-171.

- JEANNEL, R. 1956. Les Psélaphides de l'Afrique du Nord. Essai de biogéographie berbère. *Mémoires du Muséum National d'Histoire Naturelle*, Paris, n. s. (Série A: Zoologie) 14: 1-233.
- KUGELANN, J. G. 1794. Verzeichniss der in einigen Gegenden Preussens bis jetzt entdeckten Kaefer-Arten nebst kurzen Nachrichten von denselben. *Neuestes Magazin für die Liebhaber der Entomologie* 1: 513-582.
- LÖBL, I. & BESUCHET, C. 2004. Subfamily Pselaphinae Latreille, 1802 (pp. 272-329). In: LÖBL, I. & SMETANA, A. (eds). Catalogue of Palaearctic Coleoptera. Volume 2. Hydrophiloidea - Histeroidea - Staphylinoidea. *Apollo Books, Stenstrup*, 942 pp.
- MOTSCHULSKY, V. I. (de) 1860. Insectes nouveaux ou peu connus des bassins de la Méditerranée et de la mer Noire jusqu'à la mer Caspienne. *Etudes Entomologiques* 8: 119-146, 2 pls.
- NEWTON, A. F. JR. & CHANDLER, D. S. 1989. World Catalog of the Genera of Pselaphidae (Coleoptera). *Fieldiana, Zoology, New Series* 53: i-iii, 1-93.
- NORMAND, H. 1930. Nouveaux Coléoptères de l'Afrique du Nord (18^e note). *Bulletin de la Société Entomologique de France* 1930: 163-166.
- NORMAND, H. 1932. Nouveaux Coléoptères de l'Afrique du Nord (20^e note). *Bulletin de la Société Entomologique de France* 37: 14-17.

Stenotopic *Hormurus* Thorell, 1876 scorpions from the monsoon ecosystems of northern Australia, with a discussion on the evolution of burrowing behaviour in Hormuridae Laurie, 1896

Lionel MONOD^{1,2}, Mark S. HARVEY³ & Lorenzo PRENDINI²

¹ Corresponding author, Département des arthropodes et d'entomologie I, Muséum d'histoire naturelle, Route de Malagnou 1, CH-1208 Genève, Switzerland. Email: lionel.monod@ville-ge.ch

² Scorpion Systematics Research Group, Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, U.S.A. Email: lorenzo@amnh.org

³ Department of Terrestrial Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia. Email: mark.harvey@museum.wa.gov.au

Stenotopic *Hormurus* Thorell, 1876 scorpions from the monsoon ecosystems of northern Australia, with a discussion on the evolution of burrowing behaviour in Hormuridae Laurie, 1896. - Three new species from the semi-arid ecosystems of Queensland, Australia, are described in the present contribution: *Hormurus ischnoryctes* n. spec., *Hormurus macrochela* n. spec., *Hormurus ochyroscapter* n. spec. Additionally, the discovery of the first female specimens of *Hormurus longimanus* (Locket, 1995) from the Northern Territory of Australia, as well as additional diagnostic characters and locality records for this species, warranted its redescription. *Hormurus longimanus* (Locket, 1995) is reinstated as the valid name for this species and the replacement name, *Liocheles extensus* Locket, 1997 placed in synonymy. Unlike most species of *Hormurus* and of the closely related genera, *Hormiops* Fage, 1933 and *Liocheles* Sundevall, 1883, which inhabit humid tropical ecosystems (evergreen forests), the four Australian species treated here inhabit seasonally dry (monsoon) habitats, and two of these (*H. ischnoryctes* and *H. ochyroscapter*) are the first fossorial hormurids to be recorded in Australia, and the first fossorial species of *Hormurus* to be described. The four species treated here appear to be relicts of an old hygrophilous lineage that sustained a major adaptive radiation during the late Tertiary aridification of the continent. Endemism and conservation issues concerning these phylogenetically valuable species are discussed in the context of high sensitivity to habitat disturbance and high risk of extinction of stenotopic species.

Keywords: *ischnoryctes* - *longimanus* - *macrochela* - *ochyroscapter* - taxonomy - ecology - Queensland - Northern Territory.

INTRODUCTION

The hormurid scorpion genus *Liocheles* Sundevall, 1883 was recently redefined, and two genera previously synonymized with it, i.e. *Hormiops* Fage, 1933 and *Hormurus* Thorell, 1876, were resurrected on the basis of a phylogenetic analysis (Monod, 2011; Monod & Prendini, in preparation). *Hormurus* is a conspicuous element of the Australasian scorpion fauna, with eight species currently recognized, all occurring east of Huxley's (1868) line. An ongoing taxonomic revision of the three genera has uncovered an unsuspected diversity. Three new species, *Hormurus ischnoryctes* n. spec., *Hormurus macrochela* n. spec., and *Hormurus ochyroscapter* n. spec., from semi-arid ecosystems of Queensland, Australia, are described in the present contribution, raising the number of accepted species in the genus to eleven. A fourth species, *Hormurus longimanus* Locket, 1995 from the Northern Territory, is redescribed following the discovery of the first female specimens, and additional diagnostic characters and locality records are provided.

These four Australian species are remarkable in several respects: all apparently have very restricted distributional ranges, all occur in much drier habitats than most other species of *Hormurus* and of the closely related *Hormiops* and *Liocheles*, which inhabit humid tropical ecosystems (evergreen forests) throughout the Indo-Pacific region, and all have developed unique morphological and/or behavioural characters in response to their habitats. *Hormurus longimanus* and *H. macrochela* are strictly lithophilous, inhabiting the narrow cracks and crevices of weathered rock outcrops, and are characterized by extreme sexual dimorphism in the length and shape of the pedipalps. In contrast, *H. ischnoryctes* and *H. ochyroscapter* are short, robust species adapted for burrowing in the ground, with modest sexual dimorphism in the pedipalps. These two species are the first fossorial hormurids recorded from Australia, and the first fossorial species of *Hormurus* to be described. Among the three genera mentioned above, burrowing was previously reported only in the pelophilous species *Liocheles nigripes* (Pocock, 1897) (Fig. 1) from the woodlands and forests of India (Tilak, 1970). The rarity of fossorial *Hormurus* species might be attributed to their restricted distributions, which may, in turn, be related to their stenotopic substratum requirements, as observed in other fossorial hormurids (Prendini, 2001).

The four *Hormurus* species treated in the present paper appear to have evolved from more generalist lithophilous ancestors in response to the late Tertiary aridification of Australia and the concomitant contraction and fragmentation of rainforests that covered the continent throughout the Paleogene (Monod, 2011; Monod, Harvey & Prendini, in preparation). These scorpions probably represent relicts of a formerly widespread lineage that persisted in rocky habitats in forest refugia and along river systems, and are thus important for reconstructing the historical biogeography of *Hormurus* on the Australian continent.

These species of *Hormurus* are also at a greater risk of extinction than others owing to their restricted habitat requirements, limited vagility, and small isolated populations. As emphasized by Prendini (2001), substratum specialists (stenotopes) usually have more restricted distributions than substratum generalists (eurytopes), and are more vulnerable to habitat perturbation because of their lower ecological plasticity. In the monsoon ecosystems of tropical northern Australia, the small size and fragmen-



FIG. 1

Liocheles nigripes (Pocock, 1897), male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.

tation of habitats suitable for *Hormurus* species increases the vulnerability of each population to environmental stochasticity. The survival of localised populations depends entirely on the protection of their habitat islands. *Hormurus longimanus* is restricted to small patches of monsoon forests scattered along the western escarpment of the Arnhem Land Plateau, a habitat that depends entirely on rainfall and the water storage capacity of rock aquifers for its persistence. Similarly, the habitat of *H. ischnoryctes* endures the dry season by the gradual discharge of ground water stored in a nearby rock formation. The mining industry, livestock, feral animals and fire represent significant threats to these fragile habitats and consequently also to the survival of their autochthonous biota, including scorpions.

MATERIAL AND METHODS

FIELDWORK: Most specimens examined were collected during field surveys in the Northern Territory and Queensland, Australia. Scorpions were collected during the day by inspecting rock crevices and exfoliations, or by excavating burrows and at night with ultraviolet (UV) light (Stahnke, 1972) using a portable Maglite lamp equipped with a UV LED retrofit (Xenopus Electronix, Austin, TX, U.S.A.).

GEOREFERENCING: Exact geographical coordinates of collecting localities were recorded using a portable GPS device (Garmin E-trek Summit). Only coarse data, rounded to the nearest 10 seconds, are provided in the present publication following the recommendations of Chapman & Grafton (2008). Geographical coordinates for records without GPS data were traced by reference to gazetteers and the GEOnet Names Server (<http://earth-info.nga.mil/gns/html/index.html>) and are given between brackets.

MAPPING: Distribution maps were produced using ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, CA, USA) by superimposing point locality records on a SRTM 90 m (3 arc-second) digital elevation model (Jarvis *et al.*, 2008) and a SRTM 1 km (30 arc-second) global bathymetry dataset (Becker *et al.*, 2009).

ABBREVIATIONS: Collections containing material examined in the present study are abbreviated as follows: AM, Australian Museum (Sydney, New South Wales, Australia); AMNH, American Museum of Natural History (New York, U.S.A.), including tissues samples stored in the Ambrose Monell Cryocollection (AMCC); CUNY, City University of New York (New York, USA); EPA, Environmental Protection Agency (Queensland, Australia); ESV, Erich S. Volschenk private collection (Perth, Western Australia); MHNG, Muséum d'histoire naturelle (Geneva, Switzerland); MNHN, Muséum National d'Histoire Naturelle (Paris, France); NHML, Natural History Museum (London, United Kingdom); NTM, Northern Territory Museum of Arts and Sciences (Darwin, Northern Territory, Australia); QM, Queensland Museum (Brisbane, Queensland, Australia); WAM, Western Australian Museum (Perth, Western Australia).

MORPHOLOGICAL TERMINOLOGY AND MENSURATION: Morphological terminology follows Vachon (1956, 1963) for cheliceral dentition, Stahnke (1970) for pedipalp segmentation, Vachon (1974) for trichobothrial patterns, Couzijn (1976) for leg segmentation, Lamoral (1979), modified by Monod & Volschenk (2004), for

hemispermatophore morphology, and Prendini (2000) for carapace sulci and sutures, and pedipalp and metasomal carinae. The postocular carapace margin refers to a strip of the lateral margin immediately posterior to the lateral ocelli (see pcm in Fig. 4). Measurements follow Stahnke (1970) and were recorded in mm using an ocular micrometer or digital calipers.

EXAMINATION: Specimens were examined with a NIKON SMZ1500 stereomicroscope at the AMNH, and with ZEISS Stemi SV8 and SV11 stereomicroscopes at the MNHG. Ultrasonic treatment (sonication) was used to remove adhering mud and soil particles, which obscure fine details, from the tegument of specimens (Nowak *et al.*, 2008). Specimens were immersed in soapy water in a digital ultrasonic cleaner for 15-90 seconds, and the procedure repeated until satisfactorily cleaned. More, shorter rounds of sonication were conducted on smaller and older specimens to avoid damage. Specimens were rinsed with distilled water after sonication.

DISSECTION: Hemispermatophores were dissected from adult male specimens using microsurgical scissors and forceps. Paraxial organ tissue was removed manually with forceps or chemically with diluted (50%) Proteinase K (Qiagen, Venlo, The Netherlands). Hemispermatophores were placed in the Proteinase K solution in an oven at 45-50°C for 15 minutes to an hour, depending on size and degree of sclerotization. After soft tissues were sufficiently digested, the hemispermatophores were removed from the solution and rinsed with distilled water.

PHOTOGRAPHS AND ILLUSTRATIONS: High resolution images of diagnostic characters were taken under long-wave UV and visible light with a Microptics ML 1000 digital imaging system at the AMNH and a custom-built system at the MHNG. CombineZM and CombineZP (Hadley, 2005, 2009) were used to fuse images taken at different focal planes into a single image with greater depth of field. Line drawings of hemispermatophores were produced using a camera lucida mounted on the stereomicroscopes. Pencil sketches were subsequently inked and scanned for further processing and editing. Illustrations and photographs were edited (background removal and contrast adjustment) in Adobe Photoshop CS5 and plates prepared with Adobe Illustrator CS5 (both from Adobe Systems, San Jose, CA, U.S.A.). Colour drawings were produced as digital media based on scientific illustrations and photographs of live specimens to accurately represent the colours present in life.

UV FLUORESCENCE IMAGING: The macrosculpture of the tegument surface of scorpions is an important source of diagnostic and phylogenetic characters but may be difficult to examine and image under visible light as it is often obscured by pigmentation beneath the cuticle or by reflection from the shiny parts of the cuticle. UV fluorescence imaging, exploiting the fluorescence property of the epicuticle when exposed to long wave UV radiation (Lawrence, 1954; Pavan, 1954a, b, c; Pavan & Vachon, 1954; Stahnke, 1972; Stachel *et al.*, 1999), overcomes these problems and, when combined with focus-stacking, allows the production of scanning electron microscope (SEM)-quality images without the elaborate and destructive preparations required for the latter (Volschenk, 2002, 2005). The technique is now widely used in scorpion systematics (Prendini, 2003a, b, 2004, 2005a, 2006; Prendini *et al.*, 2003, 2006; Ojanguran-Affilastro *et al.*, 2007, 2009; Vignoli & Prendini, 2008, 2009; Navidpour &

Lowe, 2009). Its primary shortcoming is the need for high sensitivity settings due to the limited amount of light provided by UV flashes. However, recent technological advances in digital SLR cameras have considerably improved the resolution of images taken under low light conditions.

SCANNING ELECTRON MICROSCOPY (SEM): SEM was used to explore the fine structure of the capsular region of the hemispermatothore, using the Microscopy and Imaging Facility at the AMNH. Hemispermatothores were dehydrated in a graded alcohol series, critical point dried in a Baltec 030 critical point dryer, mounted on standard aluminium stubs (diameter 12 mm, height 7 mm; Electron Microscopy Sciences), and sputter-coated with gold/palladium in a Denton Vacuum Desktop II. Samples were examined with a Hitachi S4700 field emission SEM.

Family **HORMURIDAE** Laurie, 1896

Genus *Hormurus* Thorell, 1876

Hormurus longimanus (Locket, 1995)

Figs 2-11, Table 1

Liacheles longimanus Locket, 1995: 191-198, figs 1-14 [junior secondary homonym of *Liacheles australasiae longimanus* (Werner, 1939), here reinstated (see Remarks)]. – Kovařík, 1998: 134.

Liacheles extensa Locket, 1997: 331 (replacement name for *L. longimanus* Locket, 1995; incorrect original spelling). – Volschenk *et al.*, 2001: 162. – Monod, 2000: 86-90, pl. 31, map 10 **syn. n.**

Liacheles waigiensis (Gervais, 1843). – Volschenk *et al.*, 2001: 162 (misidentification, part).

Liacheles extensus. – Fet, 2000 (mandatory change of ending): 397. – Monod & Volschenk, 2004: 675, 686 (part).

HOLOTYPE: NTM A000196; ♂; Australia, Northern Territory, Arnhem Land, Oenpelli area [13°19'36"S, 133°03'23"E]; 21-22.VII.1992; A. Wells & J. Webber.

PARATYPE: NTM A000197; 1 ♂; Australia, Northern Territory, Kakadu National Park, 13°20'S, 139°40'E; 20.II.1994; under decaying bark in monsoon vine forest, G. Wallis.

OTHER MATERIAL: QM-S23252; 1 ♀, 1 imm.; Australia, Northern Territory, Gorge NE of Mount Gilruth [13°03'S, 133°05'E]; 10-13.VII.1979; rainforest, G. B. Monteith & D. J. Cook. – WAM 98/1852-5; 4 imm.; Kakadu National Park, Jim Jim Falls, 13°20'S, 132°50'E; 31.V.1992; under rocks, M. S. Harvey & J. M. Waldock. – WAM T129144; 1 ♂, 4 ♀, 2 imm.; idem; 21-22.VIII.2009; 64-129 m, monsoon forest, in rock crevices, G. Brown & L. Monod. – MHNG, without registration number; 1 ♂, 1 ♀; same data as previous record. – AMNH, without registration number; 1 ♂, 1 ♀; same data as previous record. – AMCC LP 10318; ♂ [1 leg], 1 imm.; same data as previous record. – WAM T129145; 1 ♀; Kakadu National Park, Koolpin Creek 13°30'S, 132°30'E; 24.VIII.2009; 107 m, vine thicket beside creek, in rock crevices, G. Brown & L. Monod. – MHNG, without registration number; 1 ♀; same data as previous record. – AMNH, without registration number; 1 ♀; same data as previous record. – AMCC LP 10317; ♀ [1 leg], ♀; same data as previous record. – WAM T129146; 2 ♂, 3 ♀, 2 imm.; Kakadu National Park, Maguk, 13°20'S, 132°30'E; 23.VIII.2009; 98 m, monsoon forest beside pools, in rock crevices, G. Brown & L. Monod. – MHNG, without registration number; 1 ♂, 1 ♀; same data as previous record. – AMNH, without registration number; 1 ♂, 1 ♀; same data as previous record. – AMCC LP 10314; ♀ [2 legs]; same data as previous record.

REMARKS: *Liacheles extensa* was introduced by Locket (1997) as a replacement name for *Liacheles longimanus* Locket 1995 to remove the secondary homonymy with *Liacheles australasiae longimanus* (Werner, 1939). *Liacheles longimanus* Locket, 1995, now transferred to the genus *Hormurus*, is no longer a junior secondary homonym of *Liacheles longimanus* (Werner, 1939) (which remains in the genus *Liacheles*),

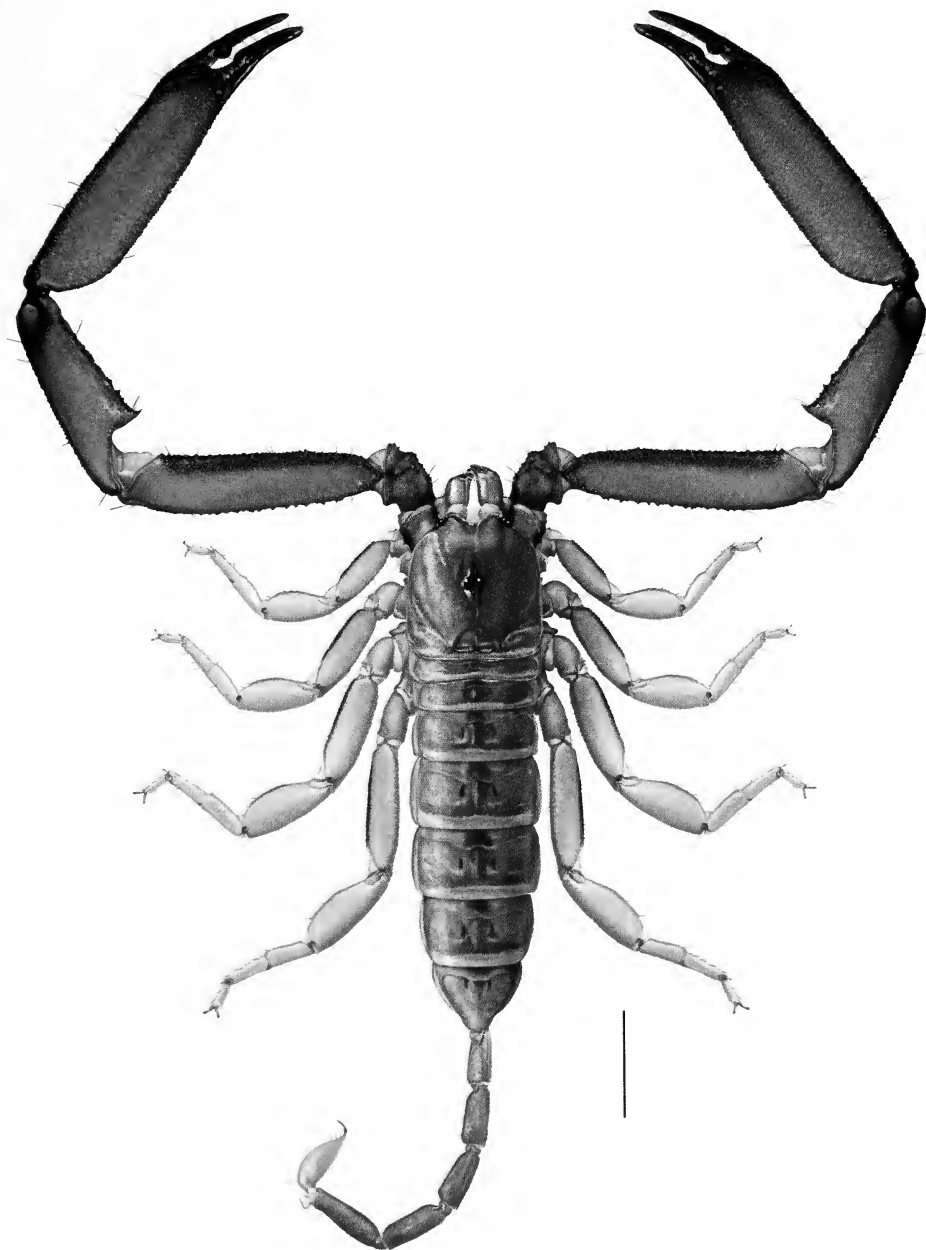


FIG. 2

Hormurus longimanus (Locket, 1995), male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.

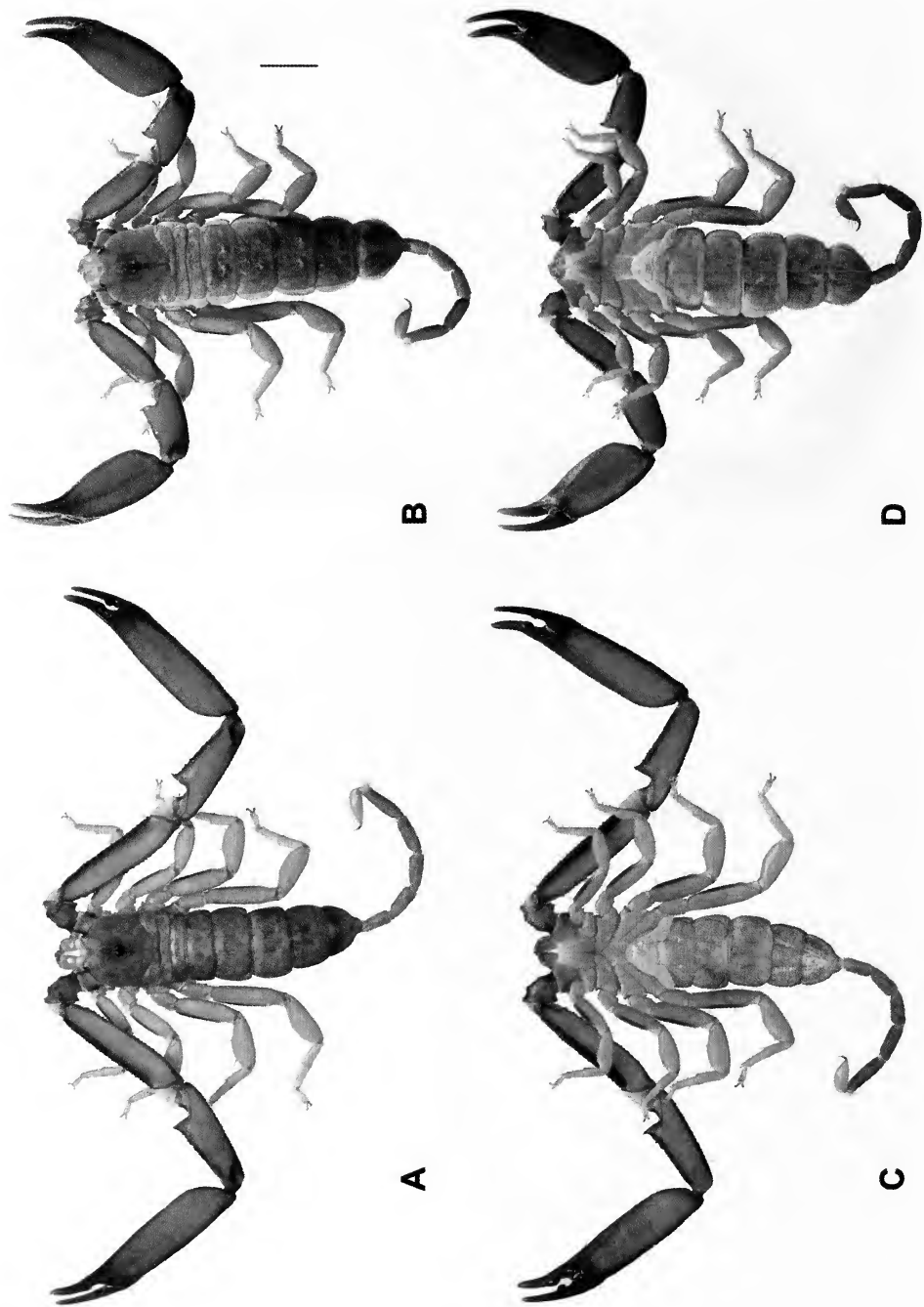


FIG. 3
Hormurus longimanus (Locket, 1995), habitus, dorsal (A, B) and ventral (C, D) aspect. (A, C) Male (MNHG). (B, D) Female (MNHG). Scale, 5 mm.

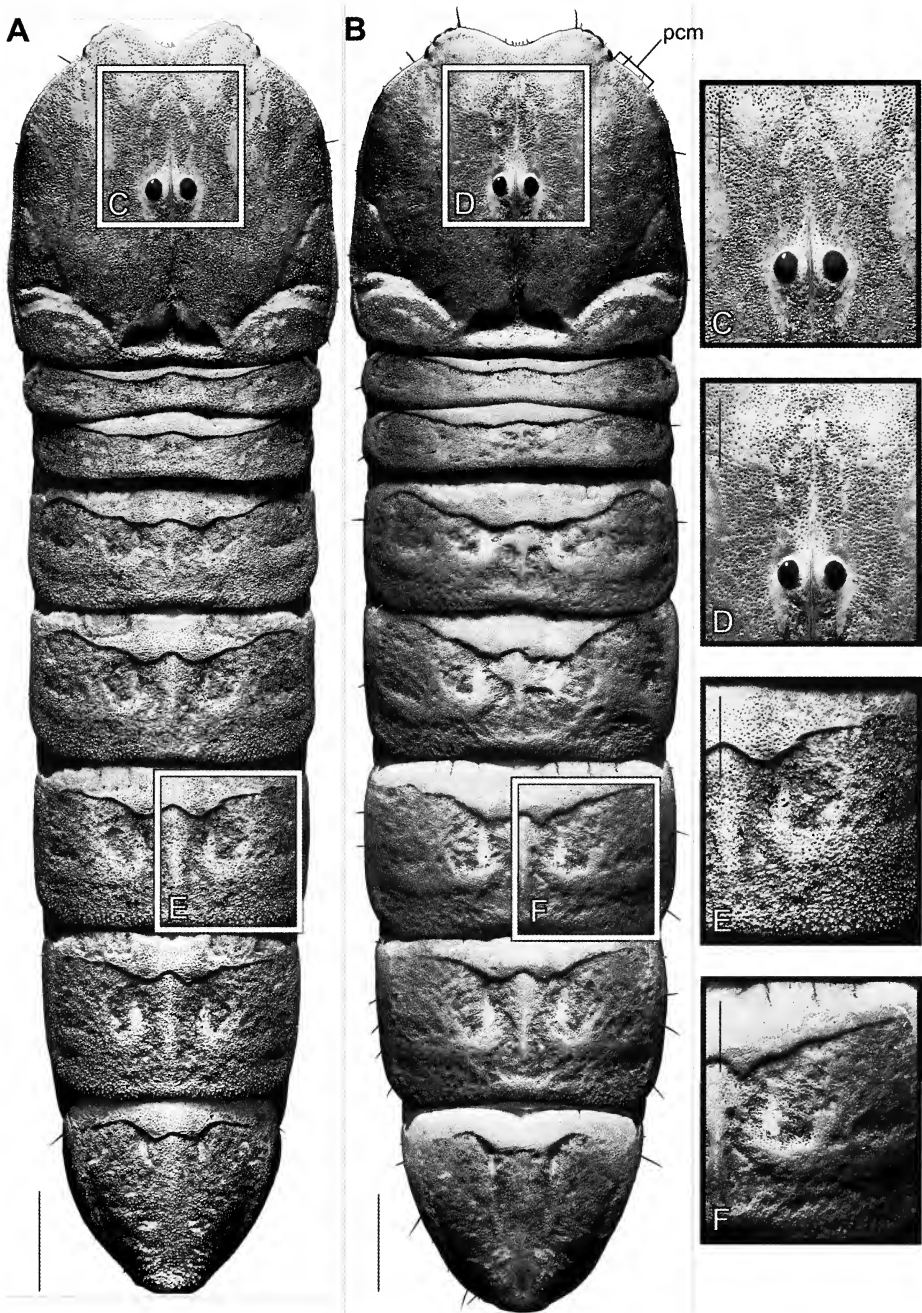


FIG. 4

Hormurus longimanus (Locket, 1995), carapace and mesosomal tergites, illustrating ornamentation and macrosculpture of cuticle (A, B), with detailed view of carapace (C, D) and tergite V (E, F), dorsal aspect. (A, C, E) Male (MNHG). (B, D, F) Female (MNHG). Abbreviation: pcm (postocular carapace margin). Scale, 2 mm (A, B), 1 mm (C-F).

and is thus reinstated in accordance with article 59.4 of the International Code of Zoological Nomenclature (ICZN, 1999). *Liocheles extensus* Locket, 1997 thus becomes a junior objective synonym of *Hormurus longimanus* (Locket, 1995).

DIAGNOSIS: *Hormurus longimanus* differs from other Australian species of the genus as follows. Sexual dimorphism of the pedipalps is more pronounced in *H. longimanus* than in other species except *H. macrochela*. The base colouration of the cuticle (tan to light brown) is much paler in *H. longimanus* than in other species except *H. ochyroscapter*. In the adult male of *H. longimanus*, the suprabasal lobe of the pedipalp chela movable finger is conical (at least as high as wide), unlike in other species in which it is rounded (wider than high); when the fingers are closed, a distinct proximal gap is evident between this lobe and the corresponding notch on the chela fixed finger in *H. longimanus*, whereas in other species the lobe and notch fit contiguously, without a proximal gap; the suprabasal lobe overlaps the retrolateral surface of the fixed finger distal to the gap in *H. longimanus*, whereas in other species there is no overlap; and the basal lobe of the chela fixed finger is extremely reduced in *H. longimanus*, compared to the well developed conical lobe observed in other species. Additionally, the dorsal surface of the chela manus is finely and densely granular in *H. longimanus*, whereas in other species the granulation is coarser. The posterior spiniform granules of the dorso-submedian carinae of metasomal segments III and IV are noticeably larger than the preceding granules in *H. longimanus*, unlike other species in which they are similar. The ventro-submedian carinae of metasomal segments I and II possess two or three pairs of well developed subposterior spiniform granules and 4-6 (I) or 4-5 (II) pairs of small median spiniform granules in *H. longimanus*, compared to other species in which the carinae possess two or three pairs of small subposterior granules and one or two pairs of small median granules. The ventrolateral carinae of metasomal segment II possess one pair of subposterior spiniform granules in *H. longimanus*, compared to other species in which the carinae possess no distinct granules.

DESCRIPTION OF ADULT MALE: *Colouration:* Dorsal surface of chelicera manus pale brown; fingers slightly darker (Fig. 2). Carapace pale brown. Pedipalps yellow to pale brown; carinae and fingers reddish brown to black. Legs pale yellow. Tergites pale brown, slightly paler than carapace; posterior margin with yellow stripe. Coxapophyses, sternum, genital operculum, pectines and sternites pale yellow. Metasoma pale brown. Telson yellow; aculeus reddish black.

Cuticle: Non-granular surfaces of carapace, pedipalps and legs, mesosoma and metasoma finely punctate.

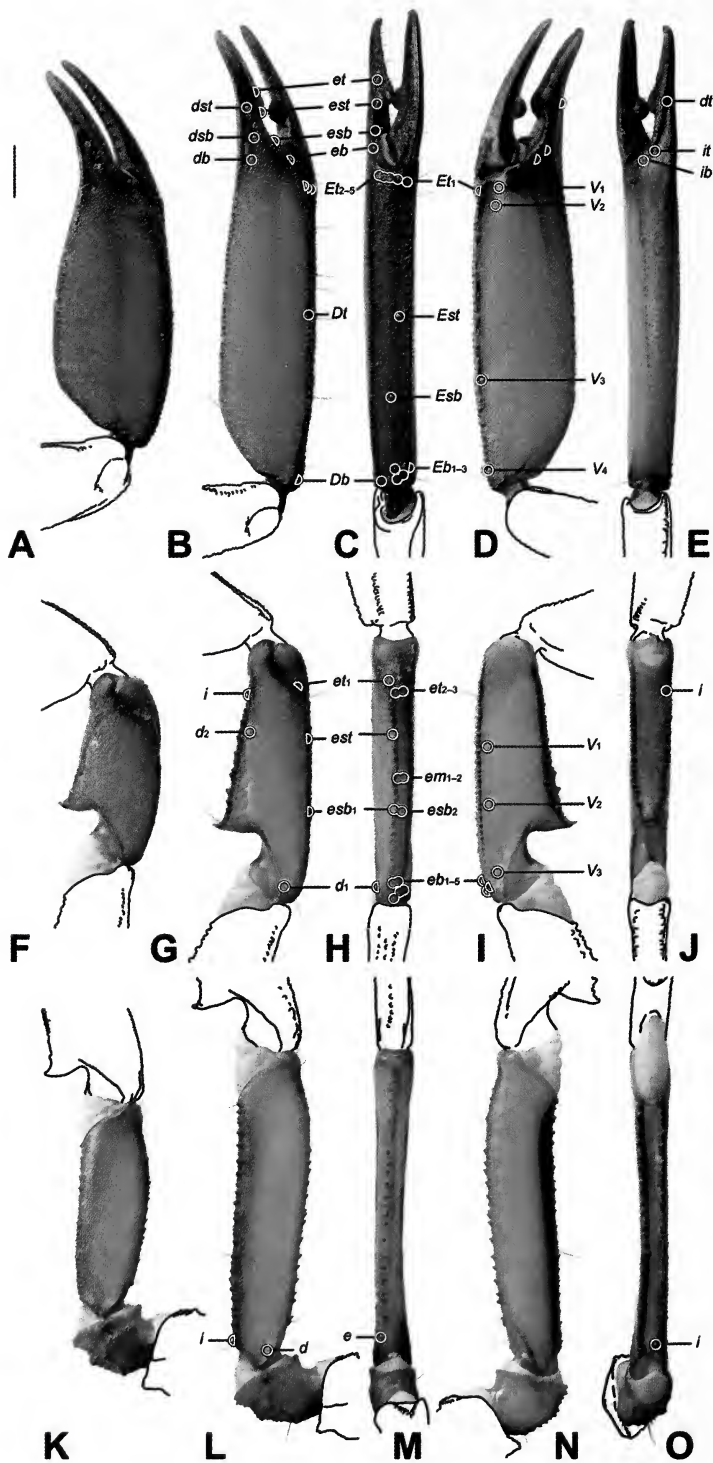
Carapace: Anterior margin with shallow median notch (Fig. 4A). Anterior furcated suture and sulci distinct. Median ocular tubercle situated anteromedially, slightly raised, small, occupying about 1/6-1/7 of carapace width; superciliary carinae present, smooth; median ocelli present, at least twice the size of lateral ocelli, separated from each other by at least half the diameter of a median ocellus. Three pairs of lateral ocelli, all equal in size, equidistant and adjacent to one another. Postocular carapace margin aspinose. Surfaces finely and densely granular (creating a matte appearance) except anteromedially, with frontal lobes smooth, fine granulation restricted to surfaces adjacent to anterior furcated sulcus and median longitudinal sulcus (Fig. 4C).

TABLE 1. *Hormurus longimanus* (Locket, 1995), measurements (in mm) of adult males and females.

Sex	♂	♂	♂	♀	♀	♀
Repository	MHNG	AMNH	AMNH	QM-S 23252	WAM	AMNH
Locality	Jim Jim Falls	Maguk	Jim Jim Falls	Mt Gilruth	Jim Jim Falls	Koolpin Creek
Total length	44	36	38	48	41	36
Carapace, length	6.0	5.8	5.8	6.9	5.9	5.7
Carapace, anterior width	3.7	3.5	3.3	4.3	3.6	3.3
Carapace, posterior width	6.6	6.3	5.9	7.1	6.6	6.1
Chela, length	18.3	16.7	16.0	16.1	13.9	13.7
Chela manus, width	3.6	3.8	3.4	4.5	4.3	4.4
Chela manus, height	1.7	1.6	1.5	1.7	1.7	1.6
Chela movable finger, length	7.1	6.7	6.3	6.8	6.0	5.8
Patella, length	10.4	9.3	8.8	8.1	7.2	6.8
Patella, width	3.0	2.9	2.8	3.4	3.2	3.1
Femur, length	12.0	10.8	10.8	9.3	8.2	8.0
Femur, width	2.7	2.8	2.5	2.9	2.8	2.5
Metasomal segment I, length	2.7	2.3	2.5	2.9	2.5	2.6
Metasomal segment I, width	1.2	1.1	1.1	1.3	1.2	1.2
Metasomal segment V, length	4.0	3.8	3.6	3.9	3.9	3.7
Metasomal segment V, width	1.1	1.0	0.9	1.0	1.0	0.9
Metasomal segment V, height	1.1	1.0	1.0	1.1	1.1	1.0
Telson vesicle, width	1.0	1.0	1.0	1.1	1.0	0.8
Telson vesicle, height	1.2	1.0	1.0	1.3	1.1	1.0

Chelicerae: Median and basal teeth of fixed finger fused into a bicuspid. Dorsal margin of movable finger with four teeth (one subdistal and one basal); dorsal distal tooth smaller than ventral distal tooth; ventral margin smooth.

Pedipalps: Pedipalp segments extremely long and slender (Figs 2, 3A, C, 5B-E, G-J, L-O, 6A), with femur length twice carapace length (Tab. 1). Chela almost asetose. **Chela fingers:** Dentate margins of fixed and movable fingers linear (without lobe and notch) distally, with two rows of primary denticles, these rows fused to each other basally; larger primary denticles located at regular intervals in each row, accessory denticles absent. Fixed finger: Suprabasal lobe reduced; suprabasal notch distinct and deep (Fig. 6A). Movable finger: Basal lobe absent or reduced to a few small spiniform granules; suprabasal lobe well developed, conical (as high as or higher than wide), gently rounded dorsally, lacking a sharp conical tooth, and overlapping retrolateral surface of fixed finger (in anterior part of notch); distinct proximal gap present between suprabasal lobe and corresponding suprabasal notch of fixed finger when fingers closed. **Pedipalp carinae:** Femur (Fig. 5L-O): Dorsoexternal carina costate, usually more distinct in proximal half; dorsointernal carina distinct, more strongly developed than dorsoexternal carina; internomedian dorsal carina obsolete, without granules; internomedian ventral carina vestigial, comprising two large spiniform granules situated proximally and medially on segment; ventromedian carina obsolete; ventrointernal carina distinct. Patella (Fig. 5G-J): Prolateral process strongly developed, forming prominent median spine; internodorsal and dorsomedian carinae distinct; dorsoexternal carina obsolete; externomedian carina granular; ventroexternal



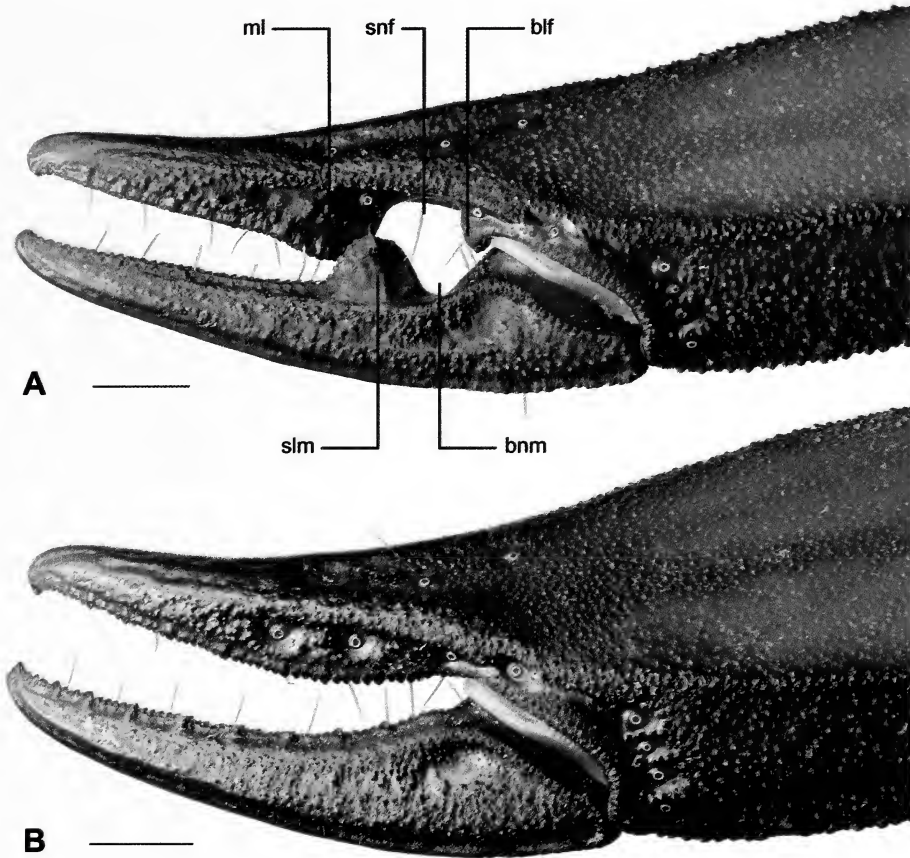


FIG. 6

Hormurus longimanus (Locket, 1995), pedipalp chela, retrolateral aspect, illustrating dentate margin of chela fingers. (A) Male (MNHG). (B) Female (MNHG). Abbreviations: blf (basal lobe, fixed finger), bnm (basal notch, movable finger), ml (median lobe), slm (suprabasal lobe, movable finger), snf (suprabasal notch, fixed finger). Scale, 1 mm.

carina distinct, granular. Chela manus (Fig. 5B-E): Dorsal secondary carina obsolete; digital carina distinct, granular, more strongly developed than external secondary carina; external secondary carina obsolete; ventroexternal carina granular to crenulate; ventromedian and ventrointernal carinae obsolete; internomedian carina distinct, granular. Pedipalp surface macrosculpture: Femur (Fig. 5L-O): Dorsal intercarinal surface finely and densely granular except distally; pro- and retrolateral intercarinal

FIG. 5

Hormurus longimanus (Locket, 1995), pedipalp chela (A-E), patella (F-J), femur and trochanter (K-O), dorsal (A, B, F, G, K, L), retrolateral (C, H, M), ventral (D, I, N) and prolateral (E, J, O) aspect, illustrating trichobothrial pattern. (A, F, K) Female (MNHG). (B-E, G-J, L-O) Male (MNHG). Scale, 2 mm.



FIG. 7

Hormurus longimanus (Locket, 1995), coxae of legs II-IV, sternum, genital operculum and pectines, ventral aspect. (A) Male (MNHG). (B) Female (MNHG). Scale, 1.5 mm.

surfaces at least sparsely granular; ventral intercarinal surface granular, distal extremity smooth. Patella (Fig. 5G-J): Dorsal, prolateral and retrolateral intercarinal surfaces finely and densely granular; ventral intercarinal surface sparsely granular, comprising a reticulated network of granules, distal margin smooth. Chela (Fig. 5B-E): Dorsal and retrolateral intercarinal surfaces of manus finely and densely granular; ventral intercarinal surface granular along pro- and retrolateral margins, smooth medially; prolateral intercarinal surface at least sparsely granular, slightly less so along ventral margin. Chela fingers granular, at least sparsely so in proximal half; *db*, *dsb* and *dst* trichobothria of fixed finger each situated in a smooth depression, surfaces around depressions granular (at least in proximal part of finger). **Trichobothria:** Pedipalps orthobothriotaxic, accessory trichobothria absent (Fig. 5B-E, G-J, L-O). Patella: *d*₂ situated distal to patellar process; five *eb* trichobothria arranged in two groups, *eb*₁ and *eb*₂₋₅ or *eb*_{1/eb}₄₋₅ and *eb*₂₋₃; two *esb* trichobothria; two *em* trichobothria; one *est* trichobothrium; three *et* trichobothria; three *V* trichobothria. Chela manus with *Dt* situated at or slightly distal to midpoint; *Eb*₃ situated close to *Eb*₁₋₂; *Esb* situated midway between *Eb* series and *Est*; *Est* situated at or near midpoint; four *V* trichobothria, with *V*₃ and *V*₄ separated. Chela fixed finger with *db* situated on dorsal surface; *eb*, *esb*, *est* and *et* equidistant (distance *esb-est* similar to distance *eb-esb*); *eb* situated at base of finger, behind point of articulation between fixed and movable fingers, aligned with *esb-et* axis; *esb* situated proximally on fixed finger, aligned with *est-et* axis; two *i* trichobothria.

Coxosternum: Leg III coxae without swelling or bulge anterodistally. Sternum equilateral pentagonal (Fig. 7A); anterior width slightly greater than posterior width; length less than or equal to posterior width.

Legs: Femora I-IV each with ventral surfaces bicarinate (proventral carinae less developed than retroventral carinae); IV with ventral carinae vestigial (only expressed distally) and indistinct, reduced to scattered granules. Retroventral margins of tibiae I and II without setiform macrosetae. Pro- and retroventral margins of basitarsi I-IV each with 4 setiform macrosetae. Telotarsi I-IV: Pro- and retroventral margins each with 4/4, 4/4, 5/5 and 5/5 setiform macrosetae (Fig. 8D, E); ventromedian row of spinules reduced to few spinules basally, terminal ventromedian spinules absent; dorsomedian lobe pronounced; laterodistal lobes truncate; unguis curved, shorter than telotarsus.

Genital operculum: Composed of two subtriangular sclerites (Fig. 7A).

Pectines: Slightly elongated, distal edge reaching but not surpassing distal edge of leg IV coxa (Fig. 7A); fulcra and two marginal lamellae present. Pectinal tooth count 6-8; teeth long and straight, entirely covered with sensory papillae.

Mesosoma: Posterior margins of pre-tergites I-VII smooth (Fig. 4A, E). Post-tergites: Posterior margins of I-VI sublinear, without distinct prominence (Fig. 4A, E); I-VI each with lateral transverse sulci; intercarinal surfaces of I and II finely and densely granular, more sparsely granular medially; intercarinal surfaces of III-VII finely and densely granular, uneven, with reticulated network of ridges and dimples. Respiratory stigmata (spiracles) of sternites IV-VI short, less than one third sternite width, and crescent-shaped, with distinct curve; sternite VII acarinate.

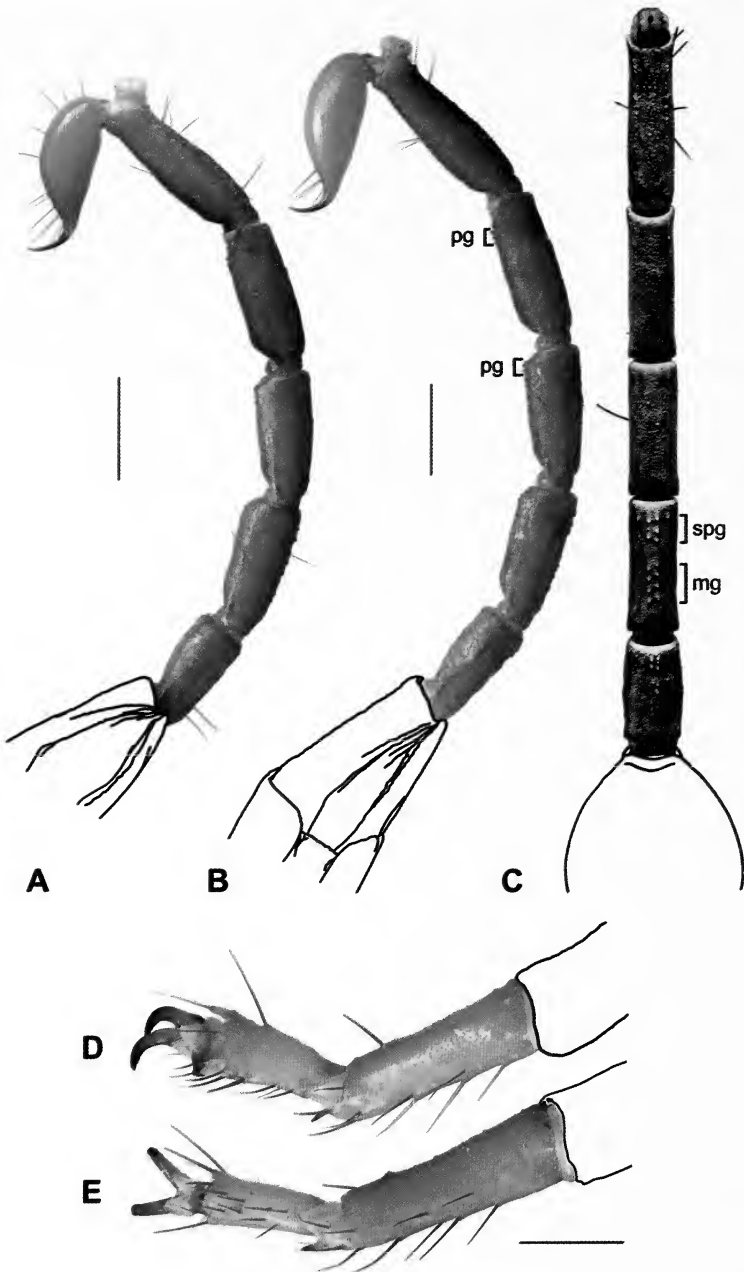


FIG. 8

Hormurus longimanus (Locket, 1995), metasoma and telson, lateral (A, B) and ventral (C) aspect, and left tarsus IV, retrolateral (D) and ventral (E) aspect. (A) Female (MNHG). (B-E) Male (MNHG). Abbreviations: mg (medial granules, ventro-submedian carinae), pg (posterior granules, dorso-submedian carinae), spg (subposterior granules, ventro-submedian carinae). Scale, 2 mm (A-C), 1 mm (D-E).

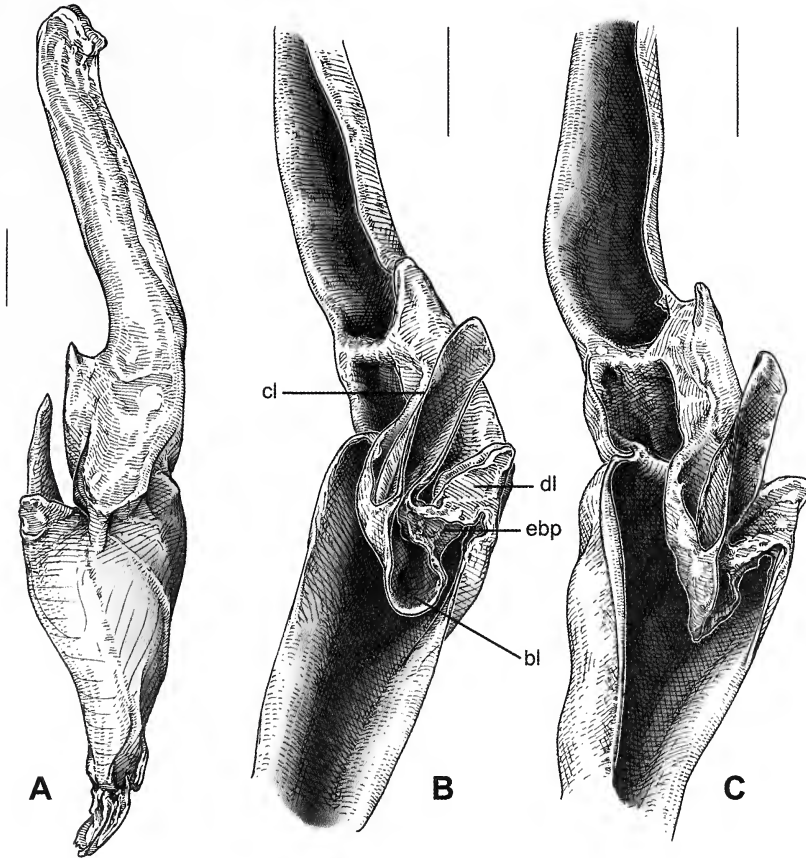


FIG. 9

Hormurus longimanus (Locket, 1995), male (AMNH), left hemispermatophore. (A) Dorsal aspect. (B, C) Detail of capsular region, ental (B) and ventral (C) aspect. Abbreviations: bl (basal lobe), cl (capsular lamella), dl (distal lobe), ebp (ental basal process). Scale, 0.5 mm.

Metasoma: Length similar to that of ♀ (Tab. 1), not flattened laterally (Fig. 8B, C), intercarinal surfaces finely and densely granular. Segments I-IV each with median sulcus distinct and deep; segment V with sulcus shallow, especially in posterior half; dorso-submedian carinae obsolete; dorsolateral, ventrolateral and ventro-submedian carinae distinct on at least some segments. Segment I: Width less than or equal to height (Tab. 1); dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; lateral median carinae distinct; ventro-submedian carinae each with 4-6 spiniform granules medially, two or three sub-posteriorly, and none posteriorly. Segment II: Dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae each with one small spiniform granule subposteriorly and none

posteriorly; each ventro-submedian carina with four or five small spiniform granules medially, two or three small spiniform granules subposteriorly, and none posteriorly. Segments III and IV: Posterior spiniform granules of dorso-submedian carinae distinctly larger than preceding granules; ventrolateral and ventro-submedian carinae weakly developed, sparsely granular, without spiniform granules. Segment V: Dorsal intercarinal surface sparsely granular; dorsolateral carinae obsolete; ventrolateral carinae weakly developed, indistinct in anterior half, granular in posterior half, granules becoming larger and spiniform posteriorly; ventromedian carina weakly developed, comprising a sparse row of spiniform granules; anal arch crenulate, comprising small denticles.

Telson: As long as or slightly longer than metasomal segment V (Fig. 8B); vesicle surfaces smooth.

Hemispermaphore (Fig. 9): Distal lamina gently curved, slightly longer than basal part of hemispermaphore; distal crest absent; single laminar hook situated in basal third, at least more proximal than midpoint; basal extrusion absent; transverse ridge distinct, approximately aligned with base of laminar hook, merging with ental edge distal to laminar hook. Capsular lamella thin, folded only proximally and unfolded distally to flattened extremity (tip and base approximately same width); longitudinal carina on dorsal surface absent to weak; accessory hook and accessory lobe absent; lamellar tip situated proximal to base of laminar hook, distal to tip of distal lobe. Distal lobe well developed, not hook-like, without accessory hook, carinae or crest. Basal lobe well developed, spoon-shaped, merging with ental basal process; ectal edge without accessory fold, forming 135-150° angle with lamella; ental edge without accessory fold toward ectal part, forming 90° angle with lamella.

DESCRIPTION OF ADULT FEMALE: As for the ♂ except as follows.

Pedipalps: All segments noticeably shorter and more robust than in male (Figs 3B, D, 5A, F, K, 6B). Dentate margins of chela fingers linear or nearly so, i.e. without pronounced lobe and notch (Fig. 6B).

Carapace: Posteromedian surface less granular than in male (Fig. 4B, D).

Genital operculum: Oval to semi-oval, as wide as long, approximately same width as sternum (Fig. 7B); opercular sclerites partly fused, median suture distinct; posterior notch present, at least weakly developed.

Pectines: Short, distal edge not reaching distal edge of coxa IV (Fig. 7B). Pectinal tooth count 5-7; teeth short and curved, sensory papillae restricted to distal part.

Mesosoma: Intercarinal surfaces of post-tergites I-VI smooth or nearly so (Fig. 4B, F); intercarinal surfaces of VII granular in posterior half only.

Metasoma: Intercarinal surfaces less granular than in male (Fig. 8A).

INTRASPECIFIC VARIATION: Pectinal tooth counts vary from six to eight in males, and from five to seven in females.

DISTRIBUTION: *Hormurus longimanus* inhabits the western escarpment of the Arnhem Land Plateau, Northern Territory, Australia (Fig. 10), and probably does not occur south of the South Alligator River. *Hormurus* has thus far not been recorded in nearby Nitmiluk National Park despite fieldwork conducted in the region by the senior author. It has also not been recorded in the northern Marrawal Plateau but it is likely to occur there.

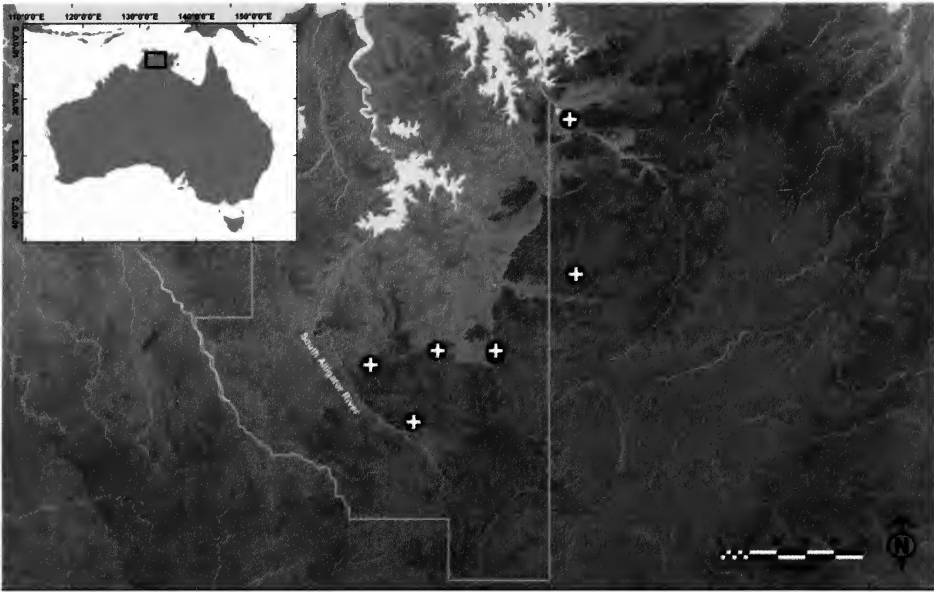


FIG. 10

Known localities of *Hormurus longimanus* (Locket, 1995) in the Northern Territory, Australia, with topography, major rivers including the South Alligator River, and boundary of the Kakadu National Park indicated.

ECOLOGY: An “archipelago” of *ca* 15,000 small patches of monsoon rainforest is scattered across the vast *Eucalyptus*-dominated landscape of predominantly savanna woodland in the Northern Territory of Australia (Russell-Smith *et al.*, 1992). Most of these patches are less than five hectares in extent, but occasionally they form extensive tracts along rivers and along the coast (Russell-Smith, 1991; Russell-Smith *et al.*, 1992). This fragmented habitat represents around 0.2% (300,000 hectares) of the total land area of the state (MPIGA, 2008). Two types of monsoon forest are recognised: wet monsoon forest occurs in areas with a perennial moisture supply, whereas dry monsoon forest occurs in well-drained areas, especially rocky areas, cliff lines and hilltops protected from recurring fires (Russell-Smith, 1991; Bowman *et al.*, 1991; Banfai & Bowman, 2006).

Hormurus longimanus is restricted to monsoon forests (mostly of the dry type) along the western edge of the Arnhem Land Plateau escarpment (Fig. 11B), which depend on orographic rainfall and the water-holding capacity of the bedrock in this predominantly rocky area (Fordyce *et al.*, 1997). The Middle-Proterozoic Kombolgie Sandstone Formation constitutes the major part of the Arnhem Plateau (Hoatson *et al.*, 2000; Johnson, 2004). The intergranular porosity of this quartz sandstone is very low (Emerson *et al.*, 1992) but the fracture system of the plateau is deep and extensive in the north and west, with an extended network of chasms, faults, gorges and fissures (Galloway, 1976; Snelling, 1992; Wyrwoll, 1992; see Fig. 11A). Rainwater accumulates in these weathered rock aquifers during the wet season, and gradually discharges



FIG. 11

Habitat of *Hormurus longimanus* (Locket, 1995) in the Northern Territory, Australia. (A) Patches of dry monsoon forest along the deeply dissected western escarpment of the Arnhem Plateau (photograph courtesy Ian Oswald-Jacobs, Parks Australia). (B) Dry monsoon forest on scree slope at Maguk.

to the surrounding habitats during the dry season. The aquifers maintain perennial seepage pools along the entire western escarpment throughout the dry season, creating a humid microclimate suitable to species like *H. longimanus* that cannot tolerate the drier conditions of the surrounding plains.

The habitat and habitus of this species are consistent with the lithophilous ecomorphotype (Prendini, 2001). All known specimens of this species were collected from narrow rock crevices and under stones near creeks and pools except the paratype, which was found under decaying bark. Specimens of lithophilous *Hormurus* species are occasionally found under the bark of logs or trees (L. Monod, personal observation). They are usually stray males that probably wandered away from the rocks seeking mates and found refuge in bark exfoliations that provide tight spaces like rock crevices.

CONSERVATION STATUS: Monsoon forest patches in the Top End of the Northern Territory are particularly vulnerable to disturbance associated with feral animals and fire (Russell-Smith & Bowman, 1992; Price *et al.*, 1995; Banfai & Bowman, 2006). In the Kakadu National Park, however, the forest patches are much larger than they were 40 years ago, mostly due to the removal of feral animals and efficient seasonal fire

management (Banfai & Bowman, 2006). The mining industry represents another potential threat to these unique habitats, especially in areas where forest patches depend on the natural discharge of ground water from nearby rock formations. Any alterations of the bedrock may have negative consequences for the water storage capacity of aquifers and ultimately for the surrounding humid habitats they sustain. As most of the known populations of *H. longimanus* lie within the boundaries of the Kakadu National Park, the species is currently not threatened by habitat destruction.

***Hormurus ischnoryctes* Monod & Prendini, n. spec.** Figs 12-21, 38B, D, Table 2

HOLOTYPE: QM; ♂; Australia, Queensland, Mount Mulligan cattle station, 16°50'S, 144°50'E; 16-17.VII.2006; 340 m, open woodland savanna, in vertical burrows 15-30 cm deep, with terminal chambers, G. Romand & L. Monod.

PARATYPES: AMNH, without registration number; 1 ♂, 4 ♀, 5 imm.; same data as holotype. – QM; 3 ♀, 4 imm.; same data as holotype. – AMCC LP 6639; 1 imm.; same data as holotype. – QM-S17140; 1 ♂; Mount Mulligan [16°51'S, 144°50'E]; 10.IX.1983; A. Williamson.

OTHER MATERIAL: MNHN RS 4209; 1 ♂, 1 ♀; Ravenshoe [145°29'0"S, 17°37'59"E]; VIII.1963; ca. 600 m, open *Eucalyptus* forest, marked cold season, low rainfall, H. St Girons.

ETYMOLOGY: The name *ischnoryctes* is constructed from the Greek words *ischnos* [thin, lean] and *oryktes* [digger]. It is an invariable noun in apposition and refers to the male pedipalps, which are unusually long and slender compared to those of other fossorial hormurids.

DIAGNOSIS: *Hormurus ischnoryctes* differs from other Australian species of the genus as follows. The base colouration of the cuticle is noticeably more reddish in *H. ischnoryctes* than in other species. The carapace is medially smooth or nearly so (only weakly granular around the median ocelli of the adult male) in *H. ischnoryctes*, whereas in other species it is granular, at least posteriorly. The prolateral process of the pedipalp patella is less developed in *H. ischnoryctes* than in other species except *H. ochyroscaptes*. Mesosomal post-tergites I-IV of the adult male are smooth medially and granular laterally in *H. ischnoryctes* whereas in other species they are completely granular. The metasomal intercarinal surfaces of the female are smooth or nearly so in *H. ischnoryctes* whereas in other species they are at least sparsely granular.

DESCRIPTION OF ADULT MALE: *Colouration*: Dorsal surface of chelicera manus orange to brown; fingers dark brown to black (Fig. 12). Carapace reddish brown, with darker areas. Pedipalps red to reddish brown; carinae and fingers reddish brown to black. Legs orange to brown. Tergites brown to dark brown, slightly paler than carapace, without red tinge. Coxapophyses, sternum, genital operculum, pectines and sternites pale orange to brown. Metasoma brown to dark brown. Telson orange to pale brown; aculeus reddish-black.

Cuticle: Non-granular surfaces of carapace, pedipalps and legs, mesosoma, and metasoma finely punctate.

Carapace: Anterior margin with shallow median notch (Fig. 14A). Anterior furcated suture and sulci distinct. Median ocular tubercle situated anteromedially, at least slightly raised, small, occupying about 1/6-1/7 of carapace width; superciliary carinae present, smooth; median ocelli present, at least twice the size of lateral ocelli, separated by at least half the diameter of a median ocellus. Three pairs of lateral ocelli,

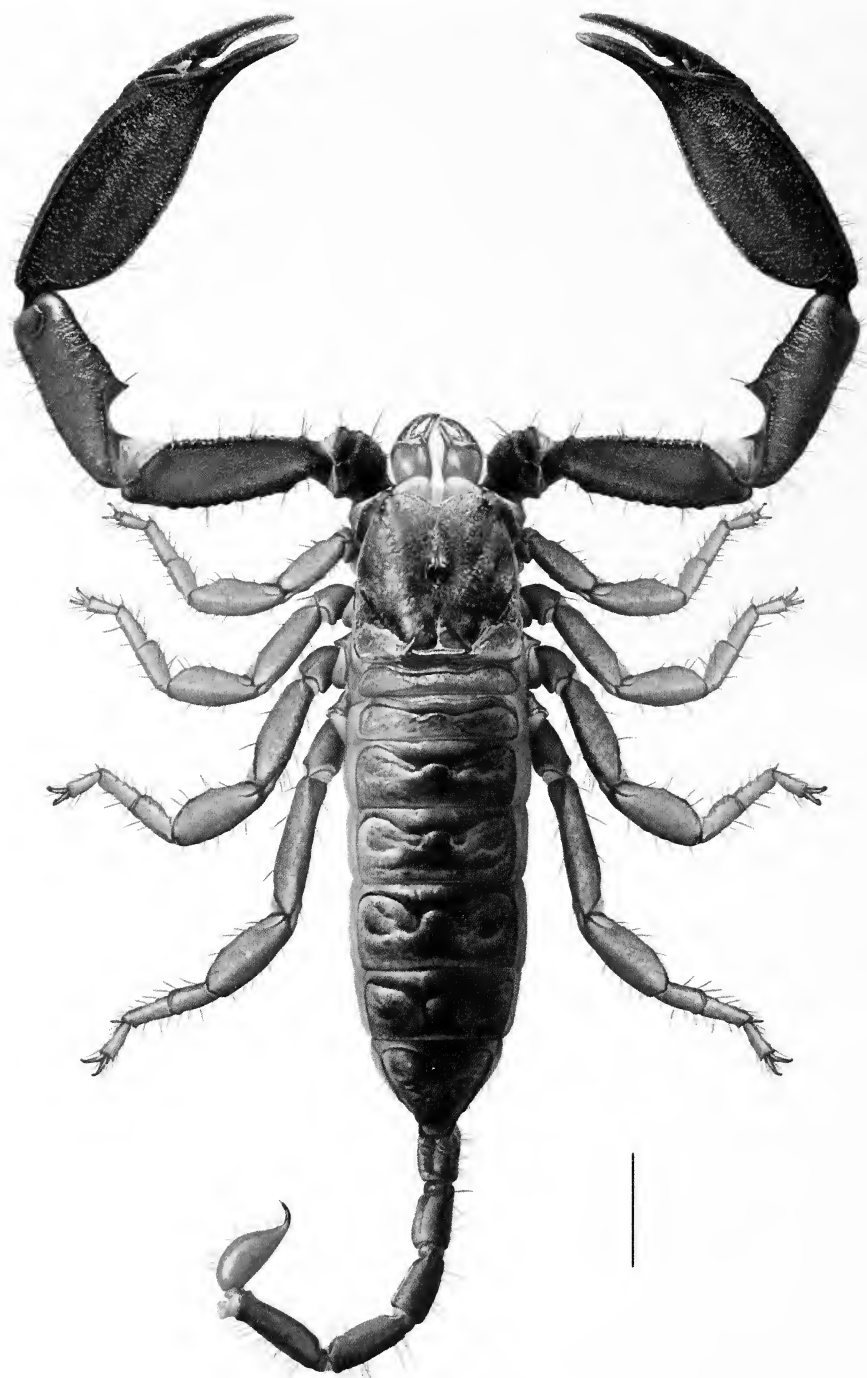


FIG. 12

Hormurus ischnoryctes n. spec., male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.

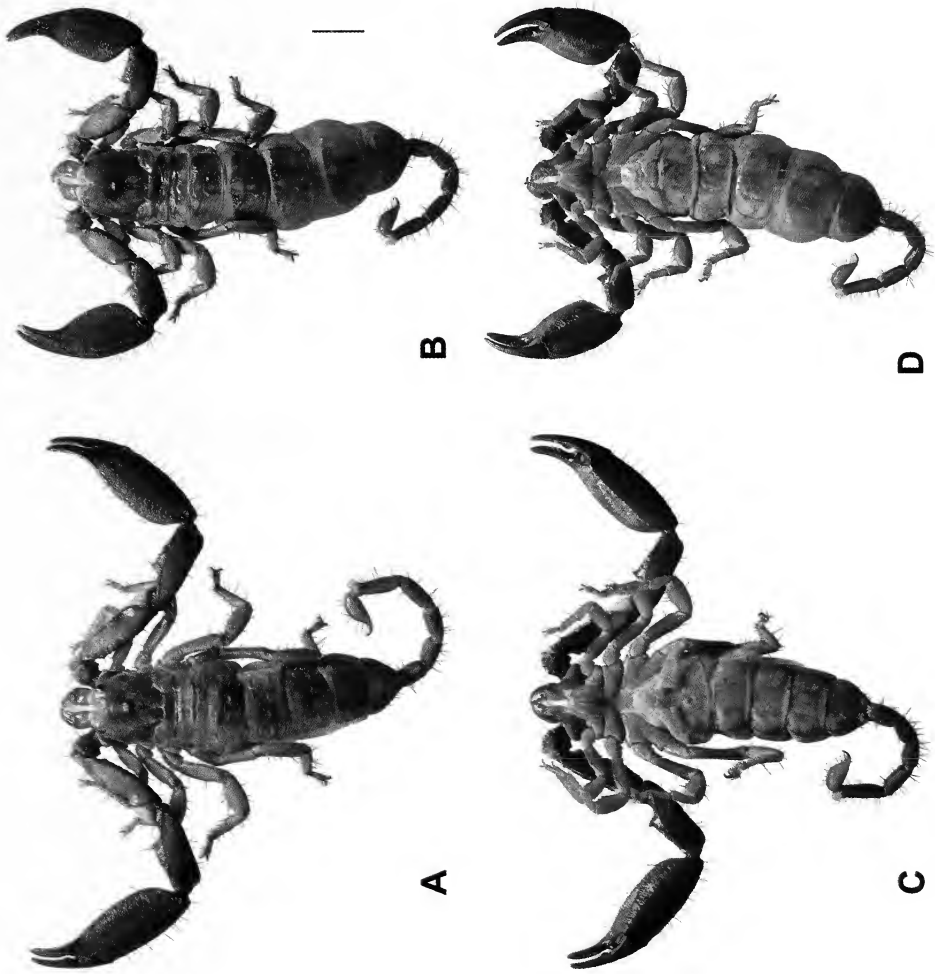


FIG. 13

Hormurus ischnoryctes n. spec., habitus, dorsal (A, B) and ventral (C, D) aspect. (A, C) Holotype male (QM). (B, D) Paratype female (QM). Scale, 5 mm.

equal in size, equidistant and adjacent to one another. Postocular carapace margin aspinose. Surfaces of frontal lobes smooth; surfaces adjacent to anterior furcated and median longitudinal sulci finely granular (Fig. 14C); median and lateral surfaces finely and at least sparsely granular; posteromedian surfaces smooth.

Chelicerae: Median and basal teeth of fixed finger fused into a bicusp. Dorsal margin of movable finger with four teeth (one subdistal and one basal); dorsal distal tooth smaller than ventral distal tooth; ventral margin smooth.

Pedipalps: All segments slightly elongated (Figs 12, 13A, C, 15B-E, G-J, L-O, 16A), with femur length slightly longer than carapace length (Tab. 2). Chela almost

TABLE 2. *Hormurus ischnoryctes* n. sp., measurements (in mm) of adult males and females.

Sex	Holotype		Paratype	Paratype	Paratype	Paratype
	♂	♂	♂	♀	♀	♀
Repository	QM	QM-S 17140	AMNH	QM	QM	AMNH
Locality	Mount Mulligan cattle station	Mount Mulligan cattle station	Mount Mulligan cattle station	Mount Mulligan cattle station	Mount Mulligan cattle station	Mount Mulligan cattle station
Total length	55.0	48.0	46.0	59.0	58.0	51.0
Carapace, length	7.2	7.6	6.8	8.1	7.9	7.8
Carapace, anterior width	5.3	5.5	4.8	5.9	5.5	5.6
Carapace, posterior width	7.6	8.7	7.2	8.4	7.8	7.7
Chela, length	17.2	17.9	15.1	16.5	14.9	14.6
Chela manus, width	4.7	4.9	4.5	5.7	5.5	5.3
Chela manus, height	3.1	3.1	2.8	3.7	3.4	3.1
Chela movable finger, length	7.6	8.5	6.9	8.4	7.6	7.1
Patella, length	9.1	9.2	7.8	7.9	7.3	7.0
Patella, width	3.6	3.6	3.1	3.8	3.7	3.4
Femur, length	9.0	9.5	7.8	7.4	7.1	6.8
Femur, width	3.0	3.0	2.7	3.2	3.0	3.1
Metasomal segment I, length	3.5	2.9	3.2	3.5	3.0	3.1
Metasomal segment I, width	1.9	2.1	1.6	2.0	1.9	2.0
Metasomal segment V, length	4.4	4.2	4.3	4.6	4.2	4.2
Metasomal segment V, width	1.2	1.4	1.1	1.3	1.3	1.3
Metasomal segment V, height	1.48	1.46	1.25	1.51	1.38	1.45
Telson vesicle, width	1.64	1.6	1.41	1.58	1.41	1.44
Telson vesicle, height	1.7	1.45	1.6	1.69	1.6	1.57

asetose. Chela fingers: Dentate margins of fixed and movable fingers linear (without lobe and notch) distally, with two rows of primary denticles, these rows fused to each other basally; larger primary denticles located at regular intervals in each row, accessory denticles absent. Fixed finger: Suprabasal lobe well developed, conical; suprabasal notch distinct and deep (Fig. 16A). Movable finger: Basal lobe absent or reduced to a few small spiniform granules; suprabasal lobe well developed, wider than high, gently rounded dorsally and lacking a sharp conical tooth, not overlapping fixed finger; suprabasal lobe and corresponding suprabasal notch of fixed finger contiguous, no proximal gap or at most a reduced gap evident when fingers closed. Pedipalp carinae: Femur (Fig. 15L-O): Dorsoexternal carina costate, usually more distinct in proximal half; dorsointernal carina distinct, more strongly developed than dorsoexternal carina; internomedian dorsal carina vestigial, without spiniform granules or with one large spiniform granule situated medially on segment; internomedian ventral carina vestigial, comprising two large spiniform granules situated proximally and medially on segment; ventromedian carina obsolete; ventrointernal carina distinct. Patella (Fig. 15G-J): Prolateral process distinct but reduced, forming single large spine; internodorsal and dorsomedian carinae distinct; dorsoexternal carina obsolete; externomedian carina granular; ventroexternal carina distinct, costate-granular. Chela manus (Fig. 15B-E): Dorsal secondary carina obsolete; digital carina distinct, granular, more strongly developed than external secondary carina; external secondary carina obsolete;

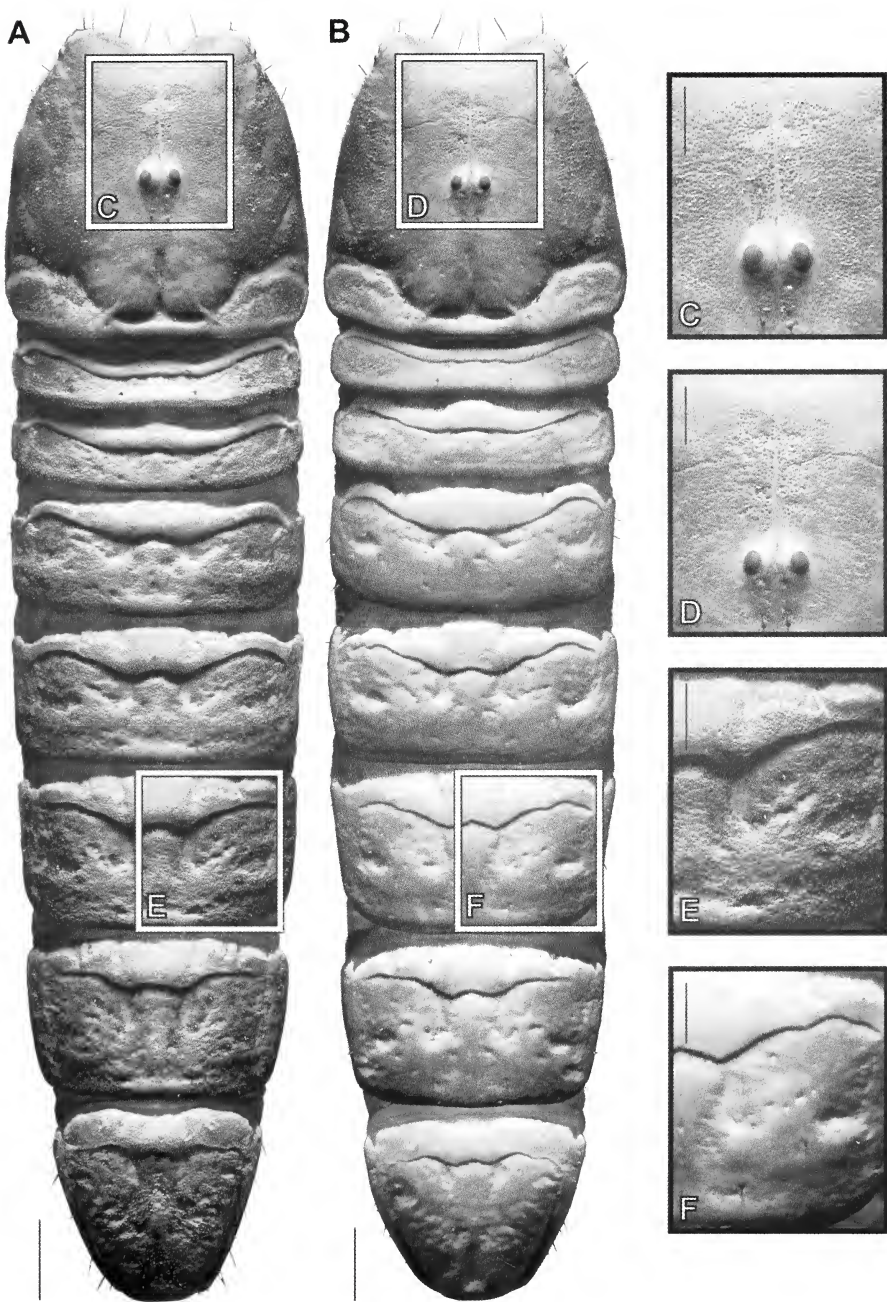


FIG. 14

Hormurus ischnoryctes n. spec., carapace and mesosomal tergites illustrating ornamentation and macrosculpture of cuticle (A, B), with detailed view of carapace (C, D) and tergite V (E, F), dorsal aspect. (A, C, E) Holotype male (QM). (B, D, F) Paratype female (QM). Scale, 2 mm (A, B), 1 mm (C-F).

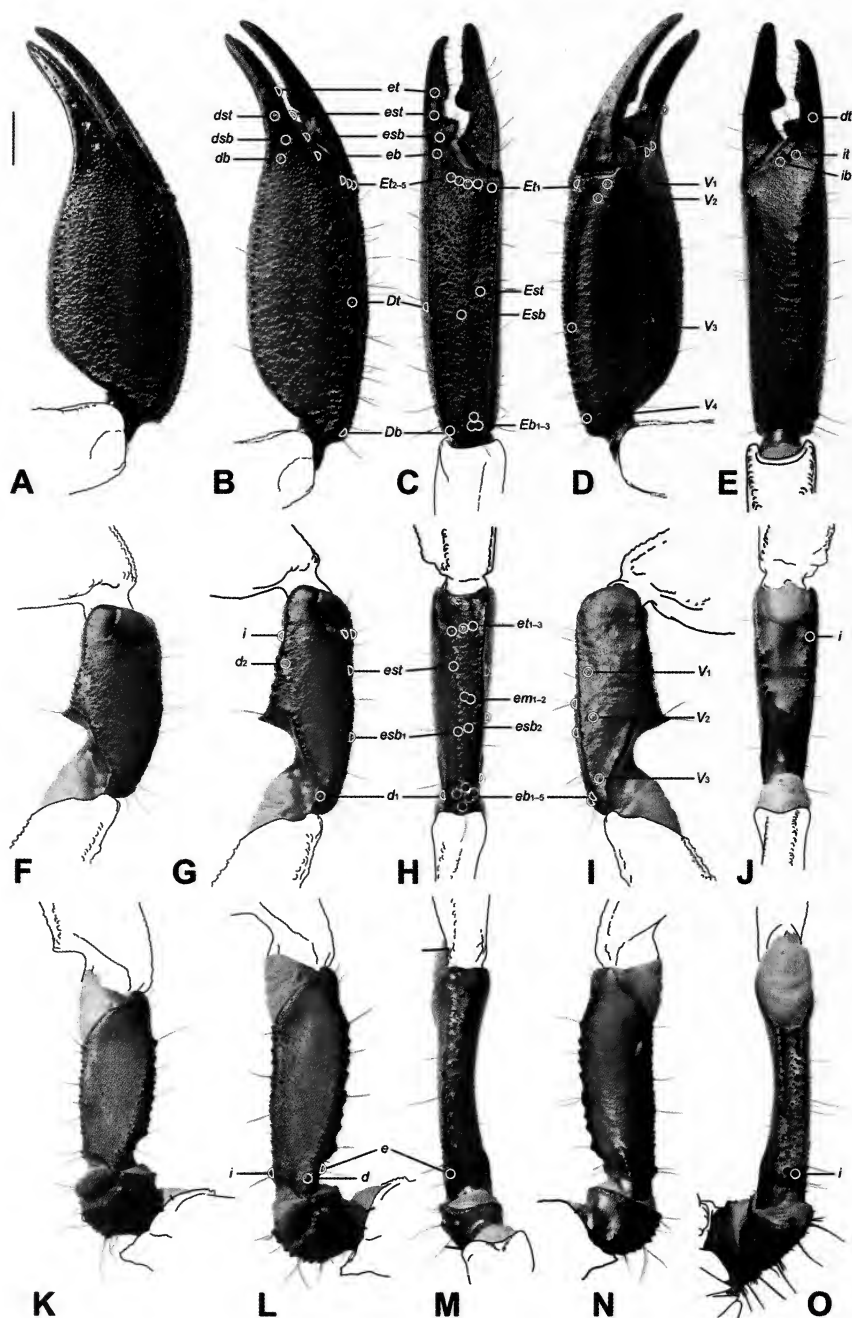


FIG. 15

Hormurus ischnoryctes n. spec., pedipalp chela (A-E), patella (F-J), femur and trochanter (K-O), dorsal (A, B, F, G, K, L), retrolateral (C, H, M), ventral (D, I, N) and prolateral (E, J, O) aspect illustrating trichobothrial pattern. (A, F, K) Paratype female (QM). (B-E, G-J, L-O) Holotype male (QM). Scale, 2 mm.

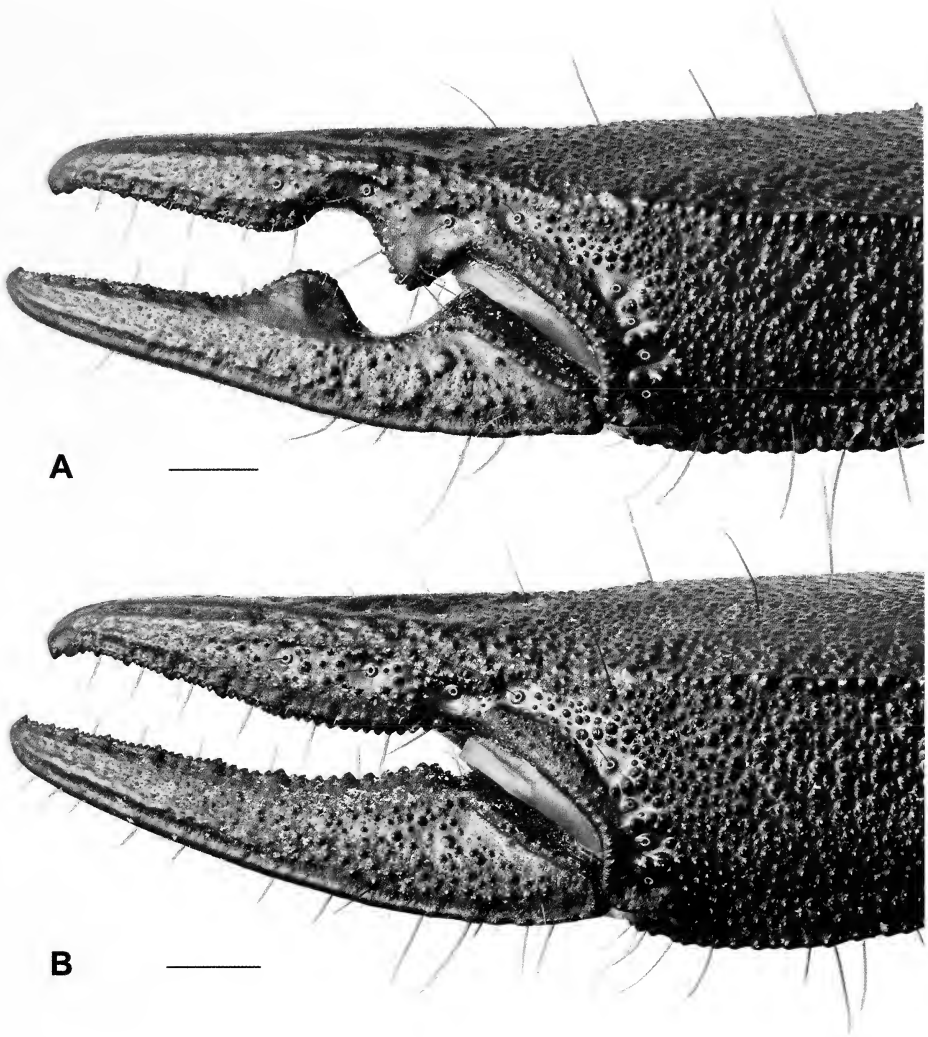


FIG. 16

Hormurus ischnoryctes n. spec., pedipalp chela, retrolateral aspect illustrating dentate margin of chela fingers. (A) Holotype male (QM). (B) Paratype female (QM). Scale, 1 mm.

ventroexternal carina granular to crenulate; ventromedian carina obsolete; ventro-internal carina reduced to row of small granules; internomedian carina distinct, sparsely granular. Pedipalp surface macrosculpture: Femur (Fig. 15L-O): Dorsal intercarinal surface densely granular except distally; pro- and retrolateral intercarinal surfaces at least sparsely granular; retrolateral intercarinal surface smooth or nearly so ventrally; ventral intercarinal surface granular proximally, smooth distally. Patella (Fig. 15G-J): Dorsal and retrolateral intercarinal surfaces granular or at least comprising a reticulated network of granules; ventral intercarinal surface sparsely granular,

distal extremity smooth; prolateral intercarinal surface sparsely granular proximally, usually less so in distal half. Chela (Fig. 15B-E): Dorsal intercarinal surface of manus densely granular, comprising medium-sized granules; retrolateral intercarinal surface granular; ventral intercarinal surface granular along pro- and retrolateral margins only, smooth medially; prolateral intercarinal surface granular. Chela fingers granular, at least sparsely so in proximal half; *db*, *dsb* and *dst* trichobothria of fixed finger each situated in a smooth depression, surfaces around depressions granular (at least in proximal part of finger). Trichobothria: Pedipalps orthobothriotaxic, accessory trichobothria absent (Fig. 15B-E, G-J, L-O). Patella *d*₂ situated distal to patellar process; five *eb* trichobothria arranged in two groups, *eb*₁ and *eb*₂₋₅ or *eb*_{1/eb}₄₋₅ and *eb*₂₋₃; two *esb* trichobothria; two *em* trichobothria; one *est* trichobothrium; three *et* trichobothria; three *V* trichobothria. Chela manus with *Dt* situated in proximal third; *Eb*₃ situated close to *Eb*₁₋₂; *Esb* situated distal to *Eb* series and close to *Est*; *Est* situated at or near midpoint; four *V* trichobothria, with *V*₃ and *V*₄ separated. Chela fixed finger with *db* situated on dorsal surface; *eb*, *esb*, *est* and *et* equidistant (distance *esb-est* similar to distance *eb-esb*); *eb* situated at base of finger, behind point of articulation between fixed and movable fingers, aligned with *esb-et* axis; *esb* situated proximally on fixed finger, aligned with *est-et* axis; two *i* trichobothria.

Coxosternum: Leg III coxae without swelling or bulge anterodistally. Sternum equilateral pentagonal (Fig. 17A); anterior width slightly greater than posterior width; length less than or equal to posterior width.

Legs: Femora I-IV each with ventral surfaces bicarinate (proventral carinae less developed than retroventral carinae); IV with ventral carinae vestigial (only expressed distally) and indistinct, reduced to scattered granules. Retroventral margins of tibiae I and II without setiform macrosetae. Pro- and retroventral margins of basitarsi I-IV each with 4 setiform macrosetae. Telotarsi I-IV: Pro- and retroventral margins each with 4/4, 4/4, 5/4-5, 5-6/5 setiform macrosetae, respectively (Fig. 18D, E); ventro-median row of spinules reduced to few spinules basally, terminal ventromedian spinules absent; dorsomedian lobe pronounced; laterodistal lobes truncate; unguis curved, shorter than telotarsus.

Genital operculum: Composed of two subtriangular sclerites (Fig. 17A).

Pectines: Slightly elongated, distal edge reaching but not surpassing distal edge of leg IV coxa (Fig. 17A); fulcra and three marginal lamellae present. Pectinal tooth count 8-10; teeth long and straight, entirely covered by sensory papillae.

Mesosoma: Posterior margins of pre-tergites I-VII smooth (Fig. 14A, E). Posterior margins of post-tergites I-VII sublinear, without distinct prominence (Fig. 14A, E); I-VI each with lateral transverse sulci; intercarinal surfaces of I-IV smooth medially, finely granular posterolaterally, at least sparsely so; intercarinal surfaces of III-VII uneven, with a distinct reticulated network of ridges and dimples; intercarinal surfaces of V-VII finely granular, at least sparsely so. Respiratory stigmata (spiracles) of sternites IV-VI short, less than one third sternite width and crescent-shaped, with distinct curve; sternite VII acarinate.

Metasoma: Length similar to that of ♀ (Tab. 2), not flattened laterally (Fig. 18B, C), intercarinal surfaces sparsely granular. Segments I-IV each with median sulcus distinct and deep; segment V with sulcus shallow, especially in posterior half; dorso-submedian carinae obsolete; dorsolateral, ventrolateral and ventro-submedian carinae

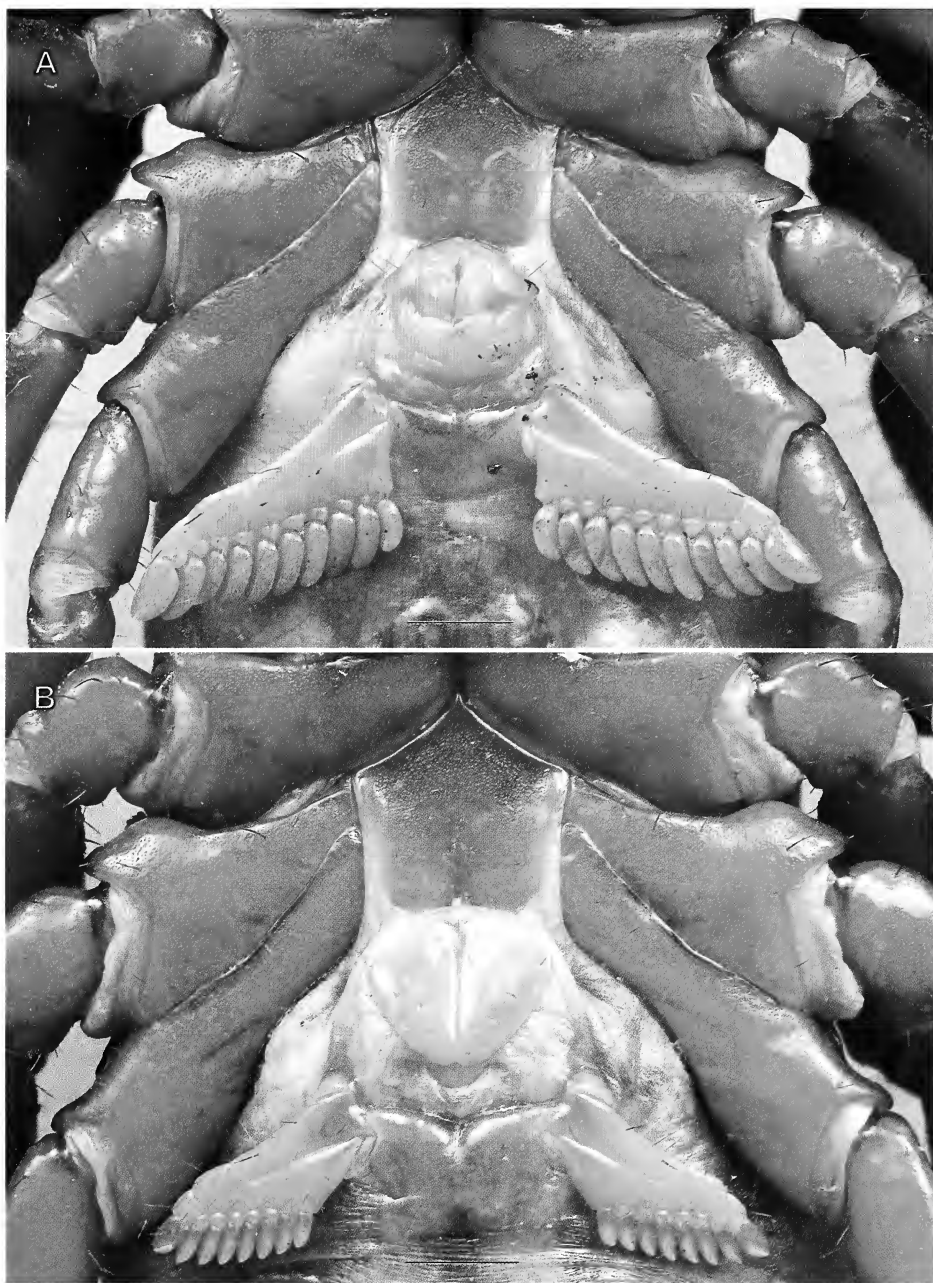


FIG. 17

Hormurus ischnoryctes n. spec., coxae of legs II-IV, sternum, genital operculum and pectines, ventral aspect. (A) Holotype male (QM). (B) Paratype female (QM). Scale, 1.5 mm.

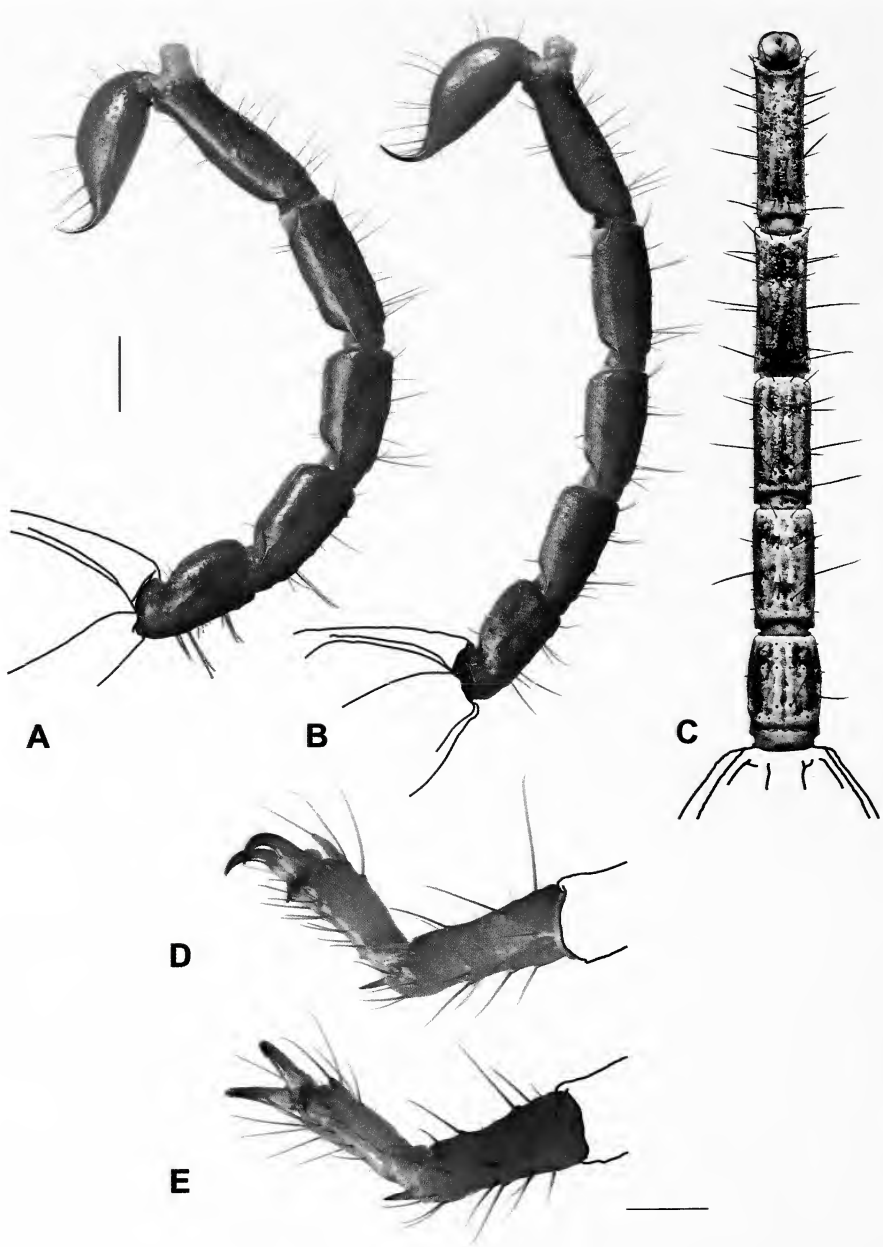


FIG. 18

Hormurus ischnoryctes n. spec., metasoma and telson, lateral (A, B) and ventral (C) aspect, and left tarsus IV, retrolateral (D) and ventral (E) aspect. (A) Paratype female (QM). (B-E) Holotype male (QM). Scale, 2 mm (A-C), 1 mm (D-E).

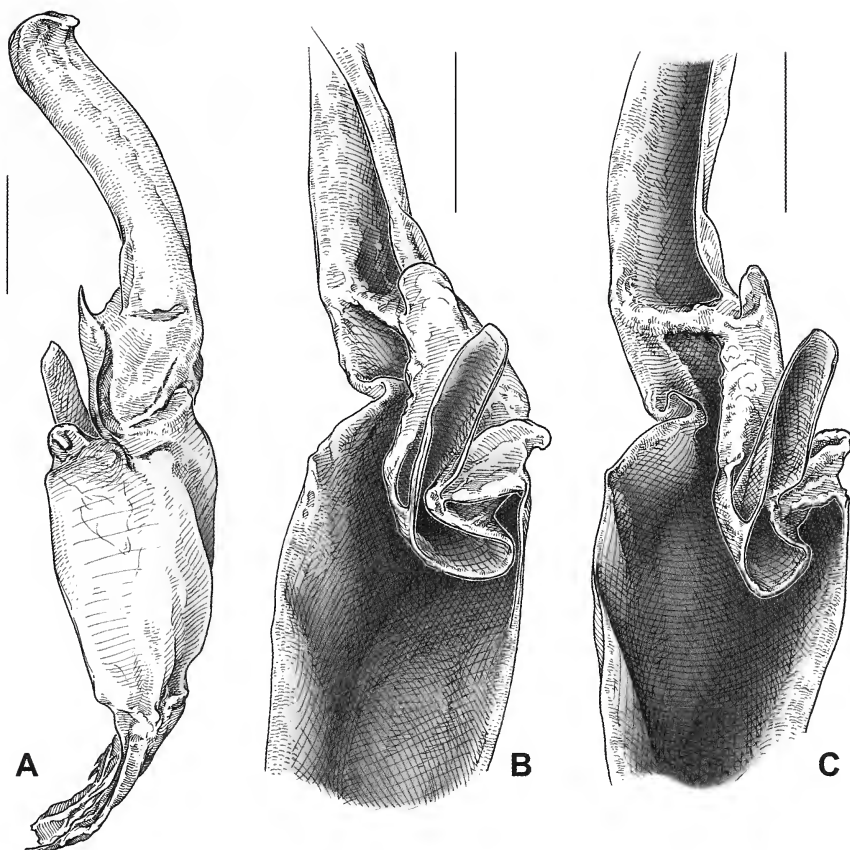


FIG. 19

Hormurus ischnoryctes n. spec., paratype male (AMNH), left hemispermatophore. (A) Dorsal aspect. (B, C) Detail of capsular region, ental (B) and ventral (C) aspect. Scale, 1 mm.

distinct on at least some segments. Segment I: Width less than or equal to height (Tab. 2); dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; lateral median carinae distinct; ventro-submedian carinae each with one or two weakly developed spiniform granules medially, one or two subposteriorly, and none posteriorly. Segment II: Dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae without spiniform granules; ventro-submedian carinae each with one or two spiniform granules medially, 1-3 subposteriorly, and none posteriorly. Segments III and IV: Posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral and ventro-submedian carinae weakly developed, sparsely granular, without spiniform granules. Segment V: Dorsal intercarinal surface sparsely granular;

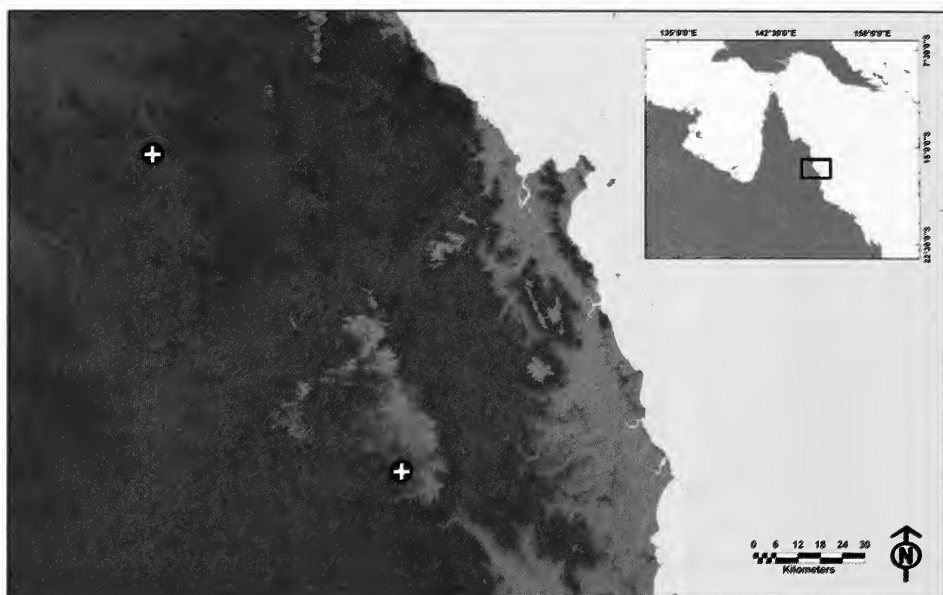


FIG. 20

Known localities of *Hormurus ischnoryctes* n. spec. in northern Queensland, Australia, with topography indicated.

dorsolateral carinae obsolete; ventrolateral carinae indistinct in anterior half, weakly developed, comprising few larger spiniform granules in posterior half; ventromedian carina weakly developed, comprising a sparse row of spiniform granules in anterior half, indistinct posteriorly; anal arch crenulate, comprising small denticles.

Telson: As long as or slightly longer than metasomal segment V (Fig. 18B); vesicle surfaces smooth.

Hemispermatorphore (Fig. 19): Distal lamina curved, slightly longer than basal part; distal crest absent; well developed single laminar hook situated in basal third; basal extrusion absent; transverse ridge distinct, approximately aligned with base of laminar hook, merging with ental edge distal to laminar hook. Capsular lamella thin, folded proximally and unfolded distally to a flattened extremity (tip and base approximately the same width); longitudinal carina on dorsal surface absent to weak; accessory hook and accessory lobe absent; lamellar tip situated slightly proximal to base of laminar hook, distal to tip of distal lobe. Distal lobe well developed, not hook-like, without accessory carinae or crest, and with moderately developed, proximad-oriented accessory hook on ental surface. Basal lobe well developed, spoon-shaped, merging with ental basal process; ectal edge without accessory fold, forming 135–150° angle with lamella; ental edge without accessory fold toward ectal part, forming 90° angle with lamella.

DESCRIPTION OF ADULT FEMALE: As for the ♂ except as follows.

Pedipalps: All segments slightly shorter and more robust than in male (Figs 13B, D, 15A, F, K, 16B). Dentate margins of chela fingers linear or nearly so, i.e. without pronounced lobe and notch (Fig. 16B).



FIG. 21

Habitat of *Hormurus ischnoryctes* n. spec. in northern Queensland, Australia. Open savanna woodland at the base of the Ngarrabullgan mesa.

Carapace: Median surface smooth or nearly so (Fig. 14B, D).

Genital operculum: Oval to semi-oval, as wide as long, approximately same width as sternum (Fig. 17B); opercular sclerites partly fused, median suture distinct; posterior notch present, at least weakly developed.

Pectines: Short, distal edge not reaching distal edge of leg IV coxa (Fig. 17B). Pectinal tooth count 7-9; teeth short and curved, sensory papillae restricted to distal part.

Mesosoma: Intercarinal surfaces of post-tergites I-VII smooth or nearly so (Fig. 14B, F); intercarinal surfaces of III-VII almost even, reticulate network of ridges and dimples obsolete.

Metasoma: Intercarinal surfaces smooth or nearly so (Fig. 18A).

INTRASPECIFIC VARIATION: Pectinal tooth counts vary from eight to ten in males, and from seven to nine in females.

DISTRIBUTION: *Hormurus ischnoryctes* was collected from open savanna woodlands west of Mareeba and the Atherton Tablelands in the North Queensland Highlands Province of Queensland, Australia (Fig. 20).

ECOLOGY: *Hormurus ischnoryctes* was collected at the base of a large Mesozoic sandstone mesa that dominates the surrounding Queensland savanna. The Pepper Pot Sandstone, dating to the early Triassic, forms the monolithic unit of this escarpment

(Bultitude *et al.*, 1997; Withnall *et al.*, 1997). As with the Arnhem Plateau, this geological formation provides orographic moisture to the surrounding habitats throughout the dry months (May to October), creating a more humid microclimate along its base and slopes that supports scattered patches of mesic vine thicket. These humid habitats form a stark contrast to the surrounding semi-arid open sclerophyll woodlands (Fig. 21) and are similar in that respect to the monsoon forest patches of the Kakadu National Park, inhabited by *H. longimanus*. *Hormurus ischnoryctes* was not collected in the vine thicket patches but at the base of the mesa, in the vicinity of a perennial pool. The burrows of this fossorial species are vertical and about 15-30 cm deep, with a slit-like entrance and an enlarged terminal chamber (Fig. 38B, D). The habitat and habitus are consistent with the pelophilous ecomorphotype (Prendini, 2001).

CONSERVATION STATUS: The only known population of this species is located on privately owned land where cattle farming is the dominant land-use, but in an area where grazing does not occur. However, the population appears to be at risk from other human activities. The coal basement of the geological formation that sustains the population was mined from 1910 to 1957, until this energy supply was replaced by a hydro-electric scheme. However, a major energy company recently resuscitated the exploitation of this coal deposit, and large-scale mining is expected to resume in the near future. No other populations of this species are known to occur within protected areas. Because of the restricted distribution of the only known population and the imminent threat of habitat destruction, it is recommended that *H. ischnoryctes* be placed on the IUCN Red List of vulnerable species (IUCN, 2001).

***Hormurus macrochela* Monod, n. spec.**

Figs 22-31, Table 3

Liocheles waigiensis: L. E. Koch, 1977 (misidentification, part): 171, 172. – Volschenk *et al.*, 2001: 162 (misidentification, part).

HOLOTYPE: QM-S59212; ♂; Australia, Queensland, Palm Island, site 4, 18°40'S, 146°40'E; 22.II.2001; 100 m, rainforest, G. B. Monteith.

PARATYPES: QM-S17042; 1 ♀, 3 imm.; Palm Island, 18°50'S, 146°40'E; L. Bancroft. – QM S17088; 1 imm.; idem; IX.1923; H. A. Longman. – QM-S59206; 1 ♂, 1 ♀; Palm Island, site 1, 18°50'S, 146°40'E; 20-21.II.2001; 450 m, rainforest, G. B. Monteith.

OTHER MATERIAL: NHML 1890.7.1.216-221; 1 ♂; Australia; Keyserling. – NHML 1925.IX.12.1-4; 1 ♂ 1 ♀, 2 imm.; Magnetic Island [19°08'19"S, 146°50'04"E]; G. F. Hill. – ESV 3370; 1 ♂; VI.1992; vine forest, E. S. Volschenk. – MHNG, without registration number; Magnetic Island, 19°10'S, 146°50'E; 4 ♂, 7 ♀, 2 imm.; 28-29.XI.2004; 41 m, vine thicket along dry creek, in rock crevices (very narrow or in between stones), R. Wyss & L. Monod. – QM; 1 ♂, 1 ♀; same data as previous record. – AMCC LP 5555; 1 imm.; same data as previous record. – NTM, without registration number; 1 ♀; Orpheus Island [18°37'20"S, 146°29'57"E]; XI.1982; R. Tiesley.

ETYMOLOGY: The name *macrochela* is constructed from the Greek words *makros* [long] and *chela* [claw]. It is an invariable noun in apposition and refers to the extreme elongation of the male pedipalps.

DIAGNOSIS: *Hormurus macrochela* differs from other Australian hormurids as follows. Sexual dimorphism of the pedipalps is more pronounced in *H. macrochela* than in other species except *H. longimanus*. The ventrointernal carina of the pedipalp chela manus is distinct and coarsely granular in *H. macrochela* whereas it is weakly developed and smooth or nearly so in other species except *Liocheles litodactylus*.

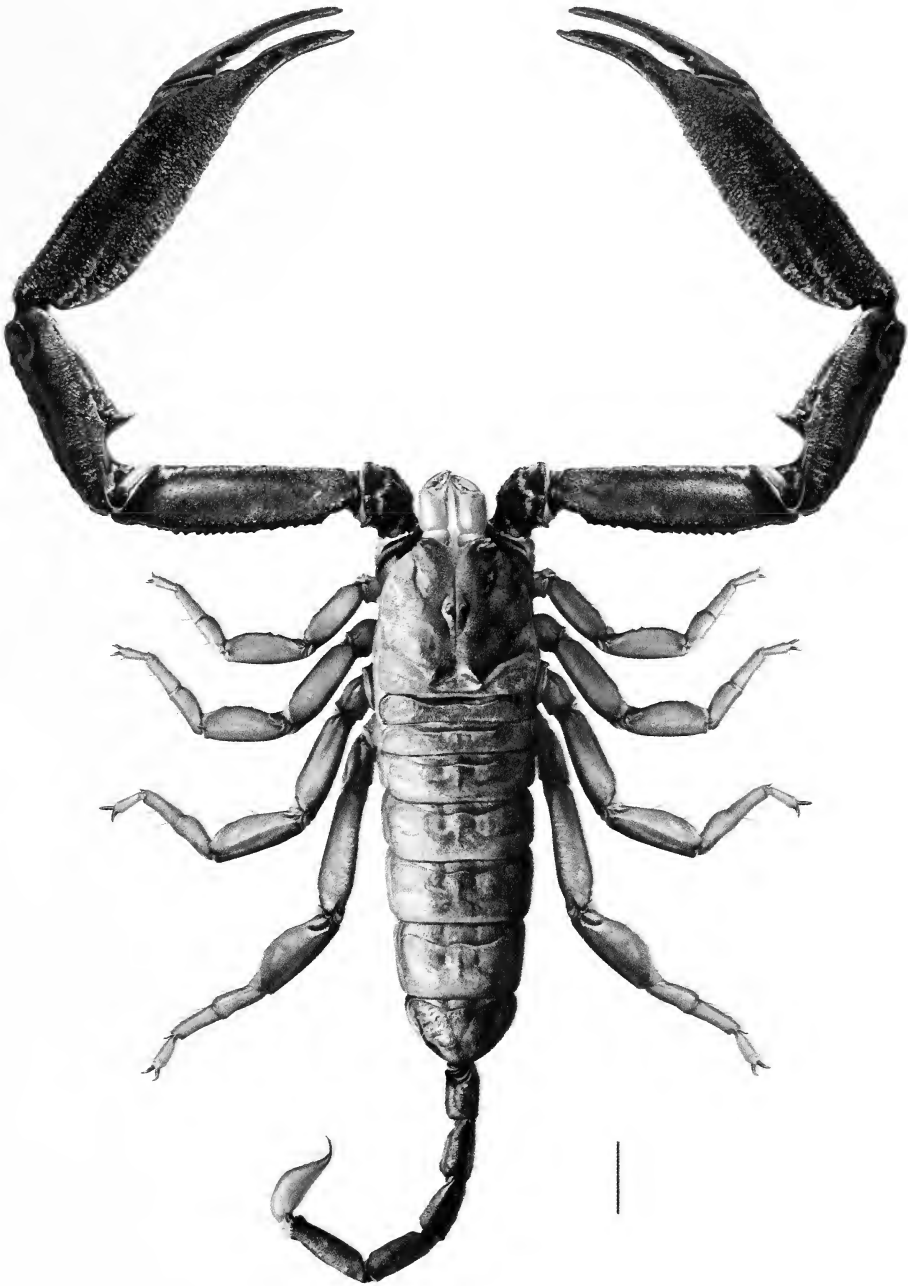


FIG. 22

Hormurus macrochela n. spec., male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.

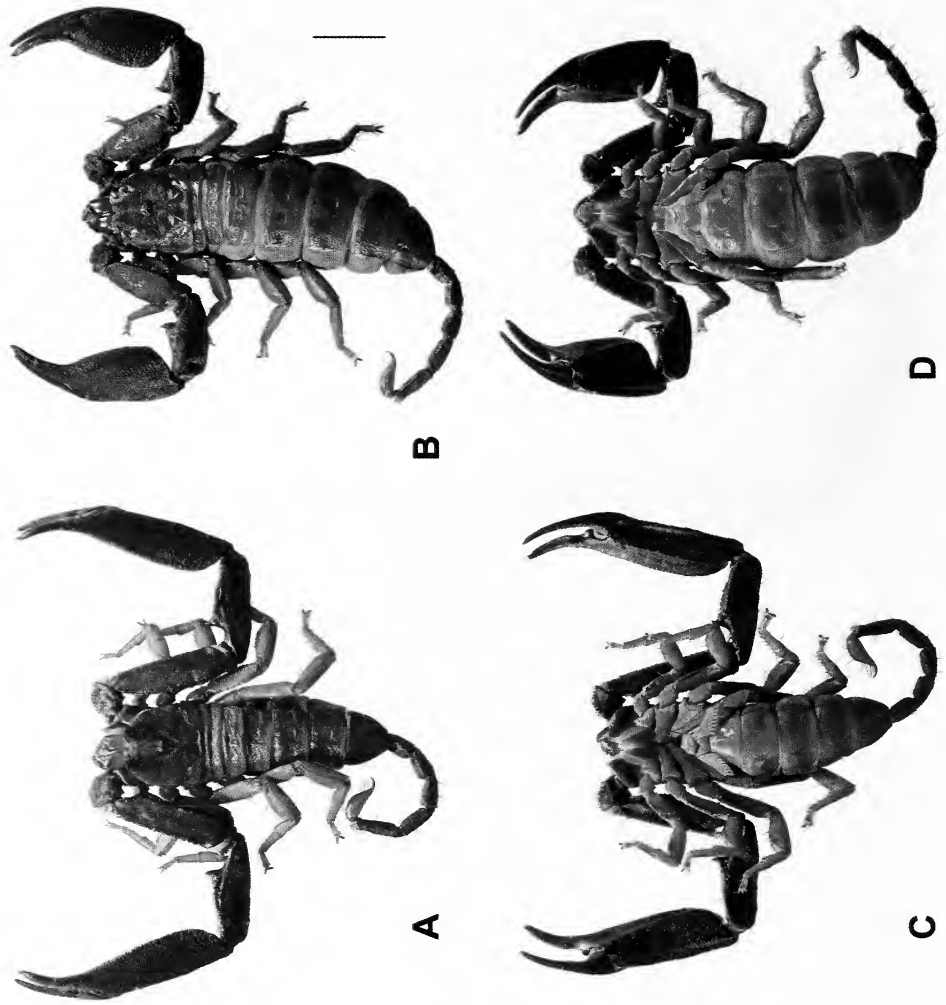


FIG. 23

Hormurus macrochela n. spec., habitus, dorsal (A, B) and ventral (C, D) aspect. (A, C) Holotype male (QM-S59212). (B, D) Paratype female (QM-S59206). Scale, 10 mm.

Monod & Volschenk, 2004. The pedipalp chela trichobothrium *Esb* is situated close to trichobothrium *Est* in *H. macrochela* whereas it is situated midway between the *Eb* group of trichobothria and *Est* in other species except *H. ischnoryctes*. The mesosomal post-tergite VII is granular at least posteriorly in *H. macrochela* but smooth or nearly so in other species except *H. longimanus*. An accessory hook, present on the ental surface of the distal lobe of the hemispermatophore capsule in *H. macrochela*, is absent in other species except *H. ischnoryctes* and *H. ochyroscapter*.

DESCRIPTION OF ADULT MALE: *Colouration*: Dorsal surface of chelicera manus orange, with darker infuscation; fingers dark brown to black (Fig. 22). Carapace dark

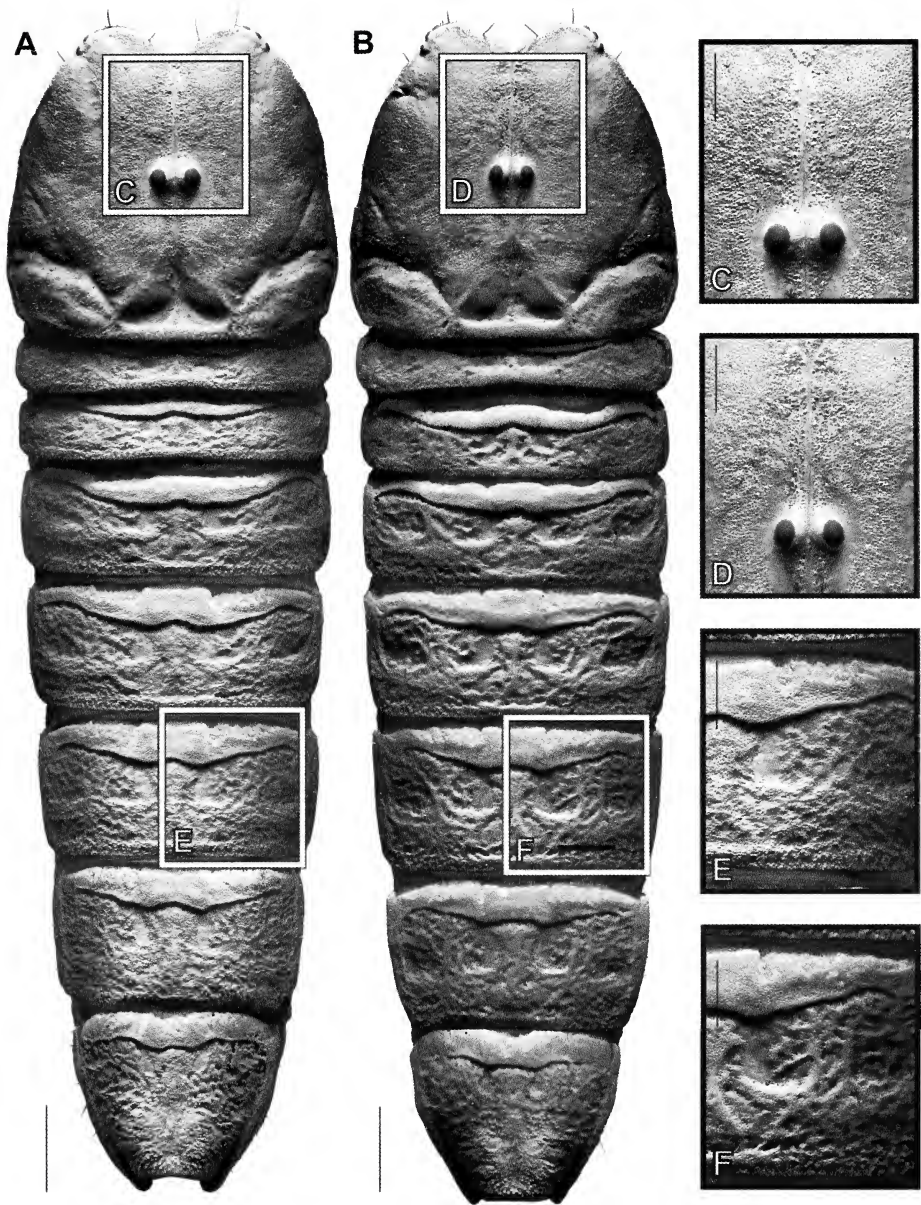


FIG. 24

Hormurus macrochela n. spec., carapace and mesosomal tergites, illustrating ornamentation and macrosculpture of cuticle (A, B), with detailed view of carapace (C, D) and tergite V (E, F), dorsal aspect. (A, C, E) Paratype male (QM-S59206). (B, D, F) Paratype female (QM-S59206). Scale, 3 mm (A, B), 1.5 mm (C-F).

reddish brown to black. Pedipalps dark reddish brown to black; carinae and fingers black. Legs pale brown. Tergites brown, paler than carapace. Coxapophyses, sternum, genital operculum, pectines and sternites orange to pale brown. Metasoma dark reddish brown to black. Telson orange; aculeus reddish-black.

Cuticle: Non-granular surfaces of carapace, pedipalps and legs, mesosoma, and metasoma finely punctate.

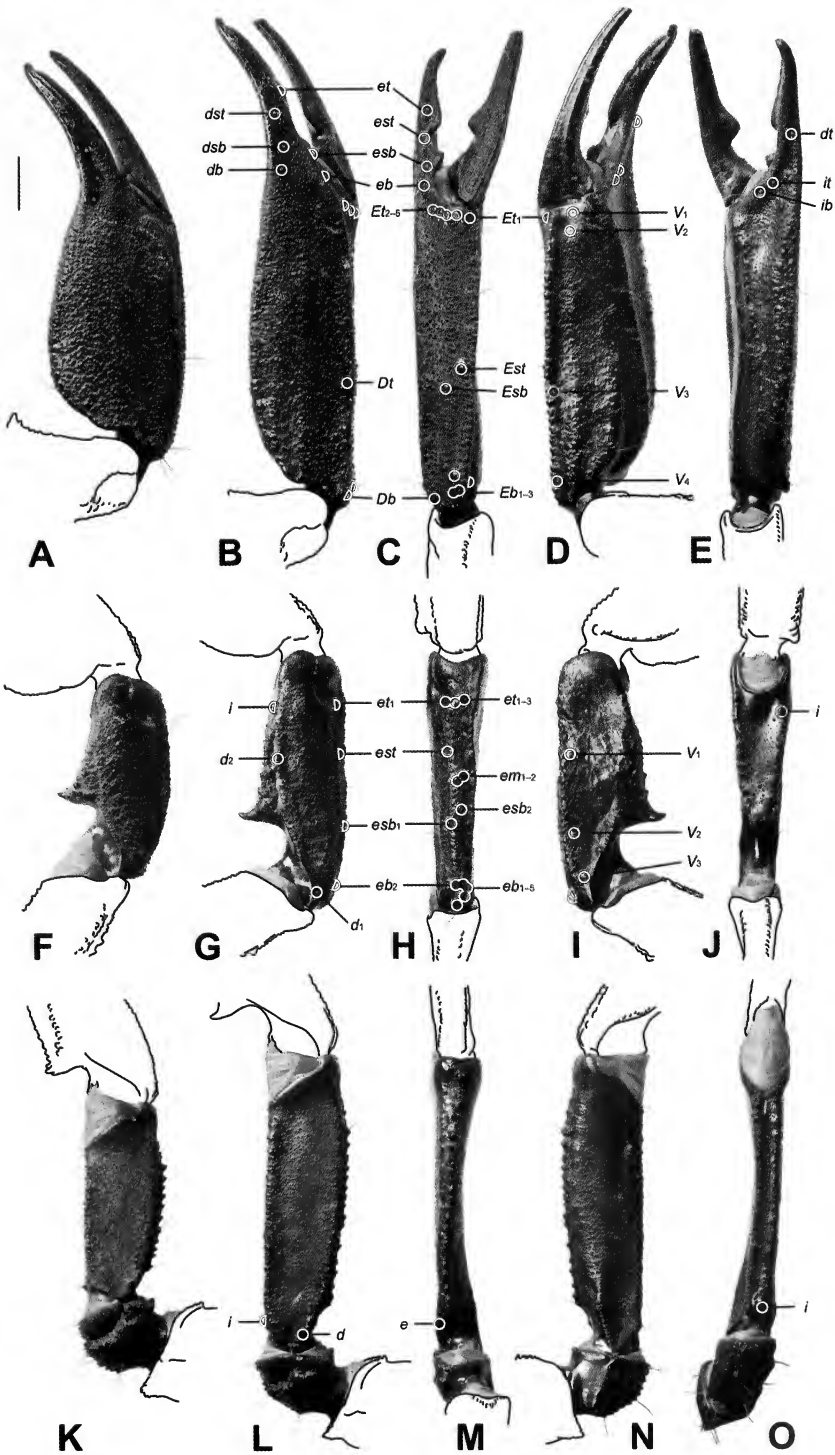
Carapace: Anterior margin with shallow median notch (Fig. 24A). Anterior furcated sutures and sulci distinct. Median ocular tubercle situated anteromedially, slightly raised, small, occupying about 1/6-1/7 of carapace width; superciliary carinae present, smooth; median ocelli present, at least twice the size of lateral ocelli, separated by at least half the diameter of a median ocellus. Three pairs of lateral ocelli, equal in size, equidistant and adjacent to one another. Postocular carapace margin aspinose. Surfaces finely granular, at least sparsely so, except anteromedially, with frontal lobes smooth and fine granulation restricted to surfaces adjacent to anterior furcated and median longitudinal sulci (Fig. 24C).

Chelicerae: Median and basal teeth of fixed finger fused into a bicuspid. Dorsal margin of movable finger with four teeth (one subdistal and one basal); dorsal distal tooth smaller than ventral distal tooth; ventral margin smooth.

Pedipalps: Segments very long and slender (Figs 22, 23A, C, 25B-E, G-J, L-O, 26A), with femur length approximately 1.5 times carapace length (Tab. 3). Chela almost asetose. *Chela fingers:* Dentate margins of fixed and movable fingers linear (without lobe and notch) distally, with two rows of primary denticles, these rows fused to each other basally; larger primary denticles located at regular intervals in each row, accessory denticles absent. Fixed finger: Suprabasal lobe well developed, conical; suprabasal notch distinct and deep (Fig. 26A). Movable finger: Basal lobe absent or reduced to a few small spiniform granules; suprabasal lobe well developed, wider than high, gently rounded dorsally and lacking a sharp conical tooth, not overlapping fixed finger; suprabasal lobe and corresponding suprabasal notch on fixed finger contiguous, no proximal gap or at most a reduced gap evident when fingers closed. *Pedipalp carinae:* Femur (Fig. 25L-O): Dorsoexternal carina costate, usually more distinct in proximal half; dorsointernal carina distinct, more strongly developed than dorsoexternal carina; internomedian dorsal and internomedian ventral carinae obsolete, without spiniform granules; ventromedian carina obsolete; ventrointernal carina distinct. Patella (Fig. 25G-J): Prolateral process strongly developed, forming a prominent median spine; internodorsal and dorsomedian carinae distinct; dorsoexternal carina obsolete; externomedian carina granular; ventroexternal carina distinct, granular. Chela manus (Fig. 25B-E): Dorsal secondary carina obsolete; digital carina distinct, granular, more strongly developed than external secondary carina; external secondary carina obsolete; ventroexternal carina granular to crenulate; ventromedian carina obsolete;

FIG. 25

Hormurus macrochela n. spec., pedipalp chela (A-E), patella (F-J), femur and trochanter (K-O), dorsal (A, B, F, G, K, L), retrolateral (C, H, M), ventral (D, I, N) and prolateral (E, J, O) aspect, illustrating trichobothrial pattern. (A, F, K) Paratype female (QM-S59206). (B-E, G-J, L-O) Holotype male (QM-S59212). Scale, 3 mm.



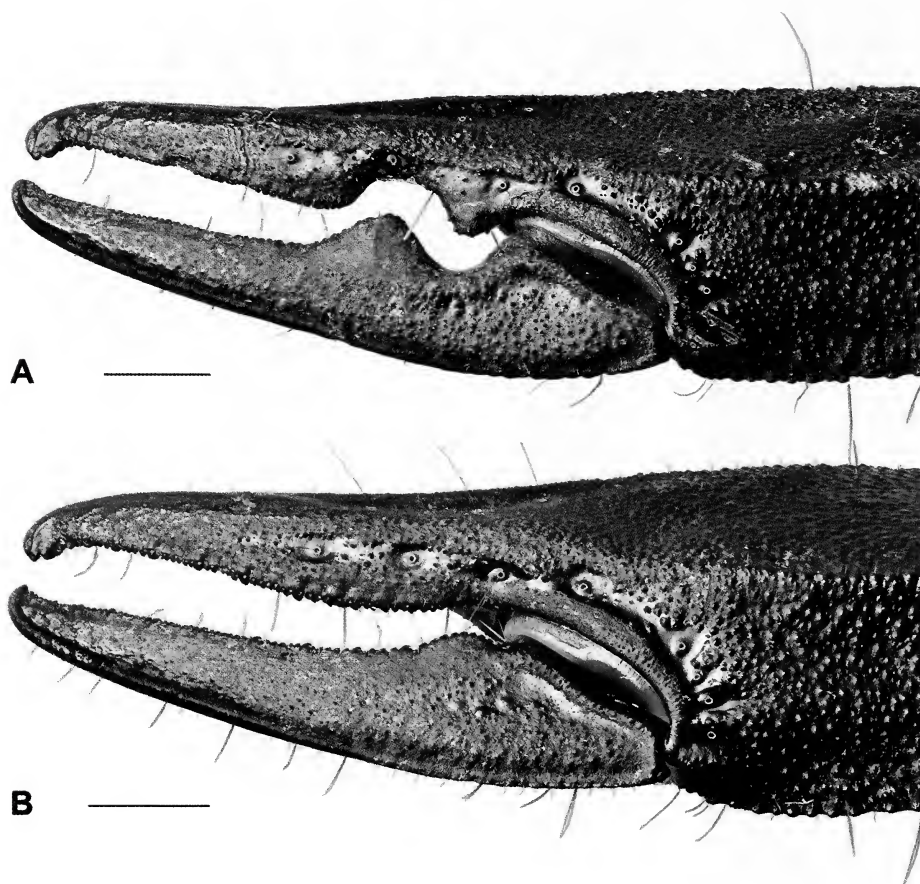


FIG. 26

Hormurus macrochela n. spec., pedipalp chela, retrolateral aspect, illustrating dentate margin of chela fingers. (A) Holotype male (QM-S59212). (B) Paratype female (QM-S59206). Scale, 2 mm.

ventrointernal carina distinct, costate-granular; internomedian carina distinct, granular, more strongly developed than ventrointernal carina. Pedipalp surface macrosculpture: Femur (Fig. 25L-O): Dorsal intercarinal surface densely granular except distally; pro- and retrolateral intercarinal surfaces at least sparsely granular; ventral intercarinal surface granular, distal extremity smooth. Patella (Fig. 25G-J): Dorsal, retrolateral and ventral intercarinal surfaces granular or at least comprising a reticulated network of granules; prolateral intercarinal surface at least sparsely granular in proximal half, usually less so in distal half. Chela (Fig. 25B-E): Dorsal and retrolateral intercarinal surfaces of manus densely granular; prolateral and ventral intercarinal surfaces at least sparsely granular. Chela fingers granular, at least sparsely so in proximal half; *db*, *dsb* and *dst* trichobothria of fixed finger each situated in a smooth depression, surfaces around depressions granular (at least in proximal part of finger). Trichobothria: Pedipalps orthobothriotaxic, accessory trichobothria absent (Fig. 25B-E, G-J, L-O).

TABLE 3. *Hormurus macrochela* n. sp., measurements (in mm) of adult males and females.

Sex	Holotype	Paratype			Paratype	
	♂	♂	♂	♀	♀	♀
Repository	QM-S5921	QM-S59206	MHNG	QM-S59206	QM-S17042	MHNG
Locality	Palm Island	Palm Island	Magnetic Island	Palm Island	Palm Island	Magnetic Island
Total length	66.0	61.0	48.0	70.0	64.0	55.0
Carapace, length	10.3	10.0	7.8	10.5	10.9	9.0
Carapace, anterior width	6.5	6.5	4.9	6.4	7.1	5.6
Carapace, posterior width	11.1	10.5	8.2	11.3	12.5	9.6
Chela, length	30.0	27.5	18.9	23.6	26.2	20.0
Chela manus, width	6.2	5.7	4.3	7.5	8.1	6.5
Chela manus, height	3.4	3.5	2.6	4.4	4.6	3.4
Chela movable finger, length	13.4	11.8	8.7	11.9	12.8	9.9
Patella, length	15.9	14.0	10.3	11.2	12.3	9.8
Patella, width	5.0	5.0	3.7	5.1	5.5	4.4
Femur, length	17.9	16.3	11.5	11.6	13.3	10.5
Femur, width	4.8	4.5	3.4	4.5	4.8	3.9
Metasomal segment I, length	3.9	3.6	2.5	3.4	4.2	3.0
Metasomal segment I, width	2.6	2.6	1.7	2.5	2.7	2.2
Metasomal segment V, length	6.4	5.8	4.8	5.7	5.7	4.6
Metasomal segment V, width	1.5	1.6	1.4	1.6	1.8	1.5
Metasomal segment V, height	1.8	1.9	1.5	1.8	2	1.6
Telson vesicle, width	1.6	1.6	1.4	1.7	1.7	1.5
Telson vesicle, height	2.0	2.1	1.5	1.8	2.1	1.8

Patella: d_2 situated distal to patellar process; five *eb* trichobothria arranged in two groups, eb_1 and eb_{2-5} or eb_1/eb_{4-5} and eb_{2-3} ; two *esb* trichobothria; two *em* trichobothria; one *est* trichobothrium; three *et* trichobothria; three *V* trichobothria. Chela manus with *Dt* situated in proximal third; Eb_3 situated close to Eb_{1-2} ; *Esb* situated distal to *Eb* series and close to *Est*; *Est* situated at or near midpoint; four *V* trichobothria, with V_3 and V_4 separated. Chela fixed finger with *db* situated on dorsal surface; *eb*, *esb*, *est* and *et* equidistant (distance *esb-est* similar to distance *eb-esb*); *eb* situated at base of finger, behind point of articulation between fixed and movable fingers, aligned with *esb-et* axis; *esb* situated proximally on fixed finger, aligned with *est-et* axis; two *i* trichobothria.

Coxosternum: Leg III coxae without swelling or bulge anterodistally. Sternum equilateral pentagonal (Fig. 27A); anterior width slightly greater than posterior width; length less than or equal to posterior width.

Legs: Femora I-IV each with ventral surfaces bicarinate (proventral carinae less developed than retroventral carinae); IV with ventral carinae vestigial (only expressed distally) and indistinct, reduced to scattered granules. Retroventral margins of tibiae I and II without setiform macrosetae. Pro- and retroventral margins of basitarsi I-IV each with 4 setiform macrosetae. Telotarsi I-IV: Pro- and retroventral margins each with 4/4, 4/4, 5/5, and 5/5 setiform macrosetae, respectively (Fig. 28D, E); ventro-median row of spinules reduced to few spinules basally, terminal ventromedian spinules absent; dorsomedian lobe pronounced; laterodistal lobes truncate; unguis curved, shorter than telotarsus.

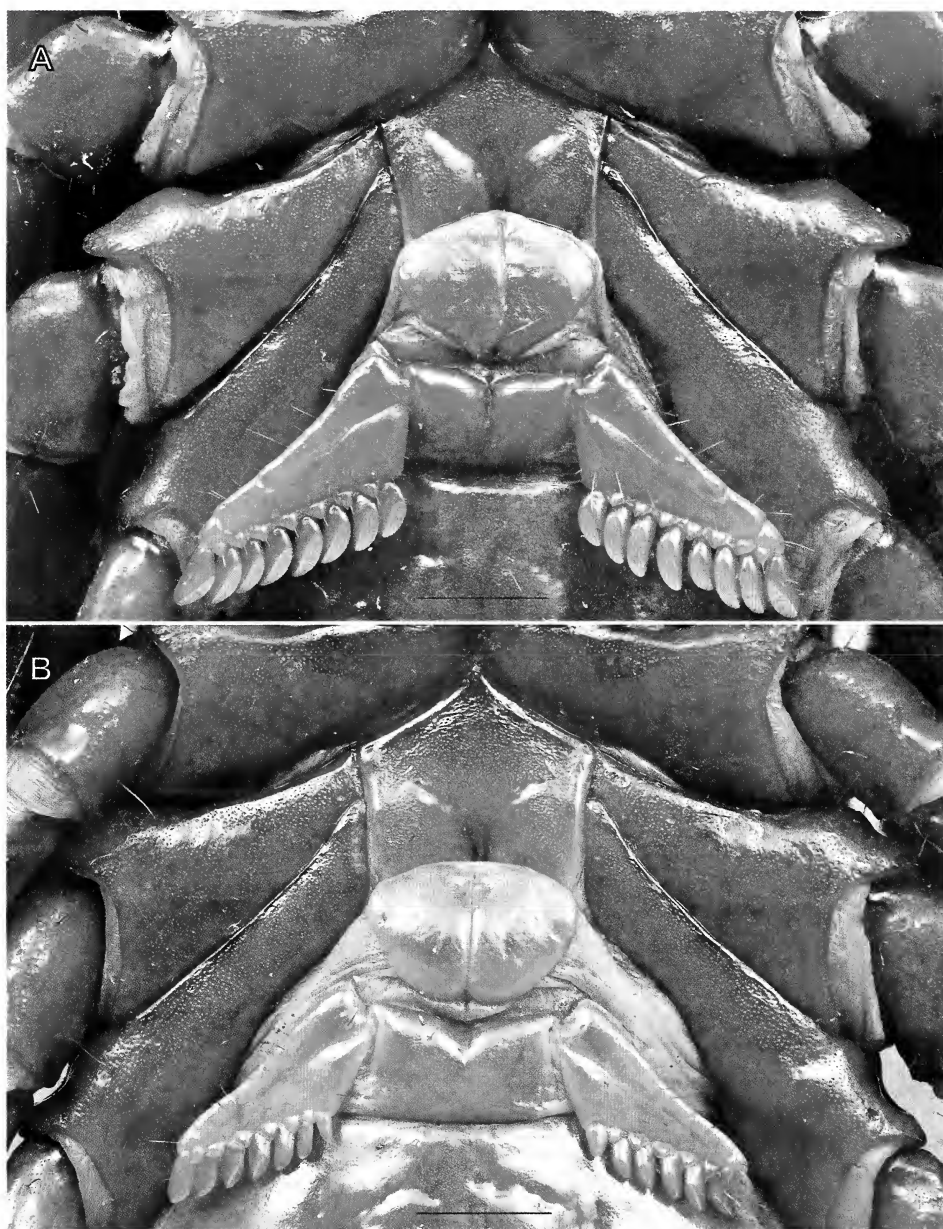


FIG. 27

Hormurus macrochela n. spec., coxae of legs II-IV, sternum, genital operculum and pectines, ventral aspect. (A) Holotype male (QM-S59212). (B) Paratype female (QM-S59206). Scale, 2 mm.

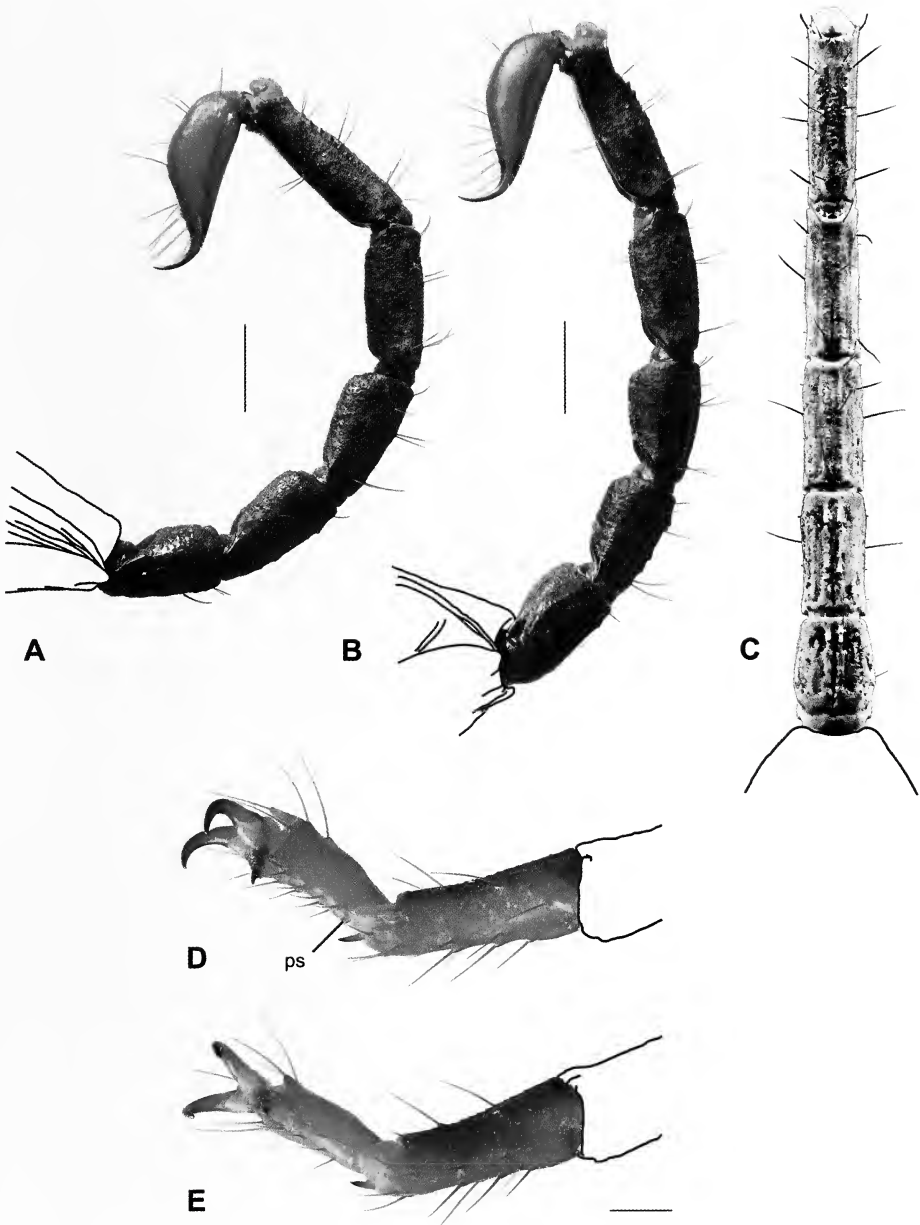


FIG. 28

Hormurus macrochela n. spec., metasoma and telson, lateral aspect (A, B) and ventral (C) aspect, and left tarsus IV, retrolateral (D) and ventral (E) aspect. (A) Paratype female (QM-S59206). (B-E) Holotype male (QM-S59212). Abbreviation: ps (proximal spinules). Scale, 3 mm (A, B), 1 mm (D, E).

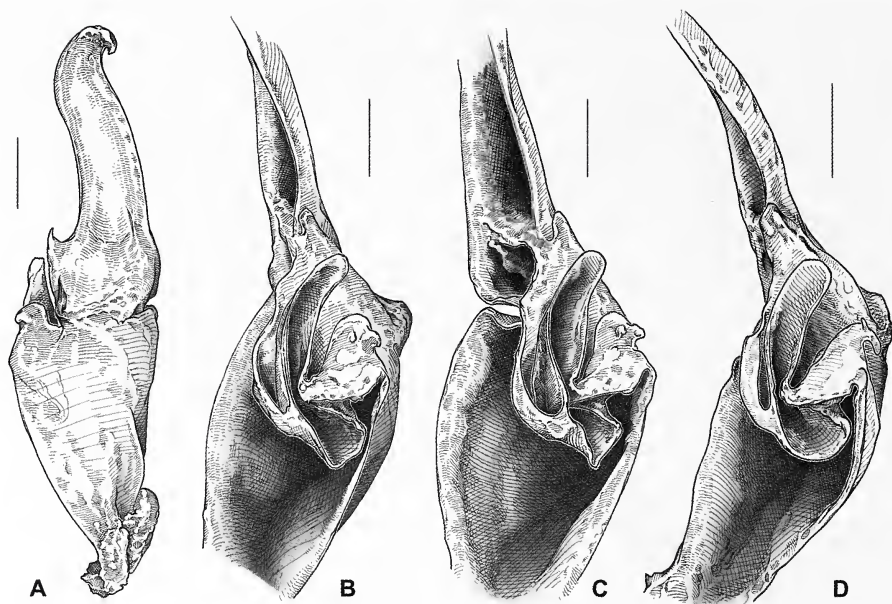


FIG. 29

Hormurus macrochela n. spec., holotype male (QM-S59212) (A-C), male from Magnetic Island (MHN) (D), left hemispermaphore. (A) Dorsal aspect. (B-D) Detail of capsular region, ental (B, D) and ventral (C) aspect. Scale, 1 mm.

Genital operculum: Composed of two subtriangular sclerites (Fig. 27A).

Pectines: Pectines slightly elongated, distal edge reaching but not surpassing distal edge of leg IV coxa (Fig. 27A); fulcra and three marginal lamellae present. Pectinal tooth count 7-9; teeth long and straight, entirely covered with sensory papillae.

Mesosoma: Posterior margins of pre-tergites I-VII smooth (Fig. 24A, E). Posterior margins of post-tergites I-VII sublinear, without distinct prominence (Fig. 24A, E); I-VI each with lateral transverse sulci; intercarinal surfaces of I-VII finely granular, at least in posterior half, more sparsely granular medially on I-III; intercarinal surfaces of III-VII uneven, with a distinct reticulated network of ridges and dimples. Respiratory stigmata (spiracles) of sternites IV-VI, short, less than one third sternite width and crescent-shaped, with distinct curve; sternite VII acarinate.

Metasoma: Length similar to that of ♀ (Tab. 3), not flattened laterally (Fig. 28B, C), intercarinal surfaces sparsely granular. Segments I-IV each with median sulcus distinct and deep; segment V with sulcus shallow, especially in posterior half; dorso-submedian carinae obsolete; dorsolateral, ventrolateral and ventro-submedian carinae distinct on at least some segments. Segment I: Width less than or equal to height (Tab. 3); dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; lateral median carinae distinct; ventro-

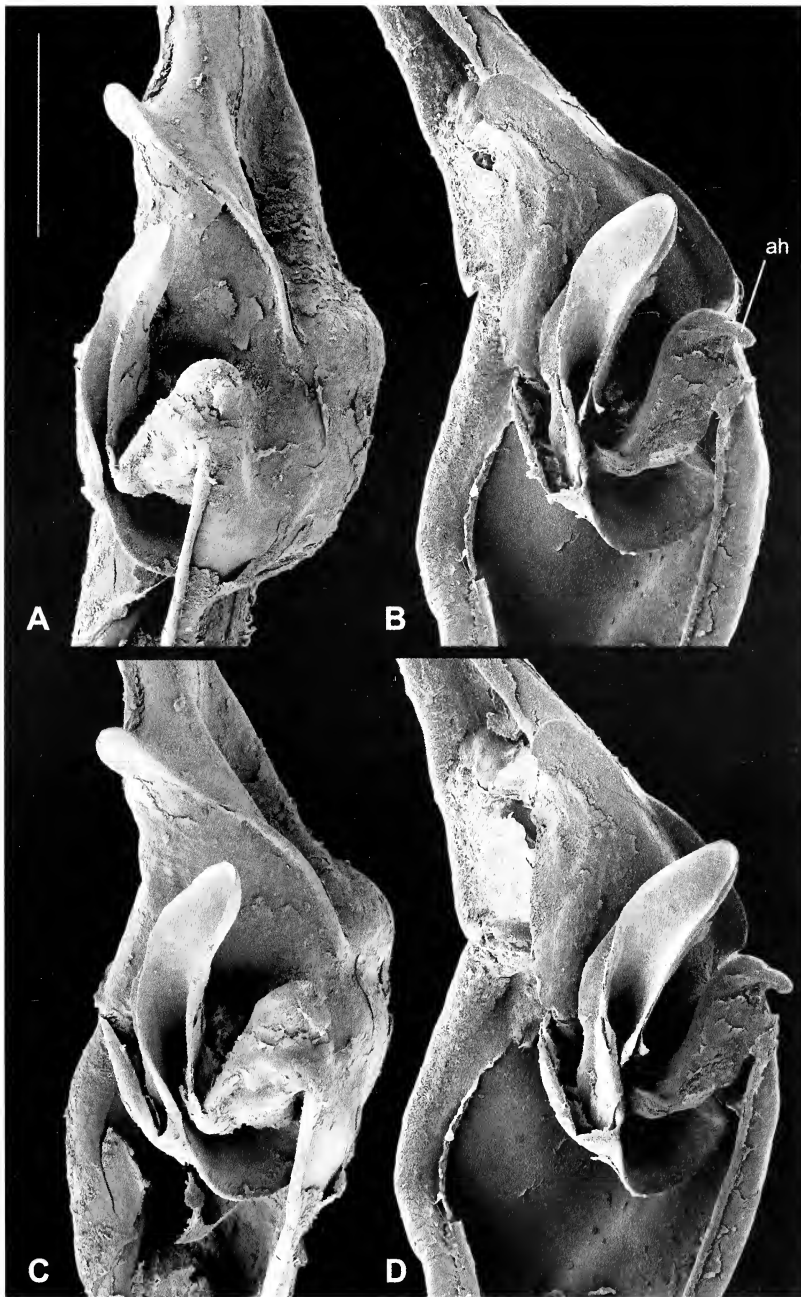


FIG. 30

Hormurus macrochela n. spec., male from Magnetic Island (MHN), left hemispermatophore, detail of capsular region. (A) Rotated approximately 30° clockwise from ental aspect. (B) Rotated approximately 30° counter-clockwise from ental aspect. (C) Ental aspect. (D) Ventral aspect. Abbreviation: ah (accessory hook). Scale, 1 mm.

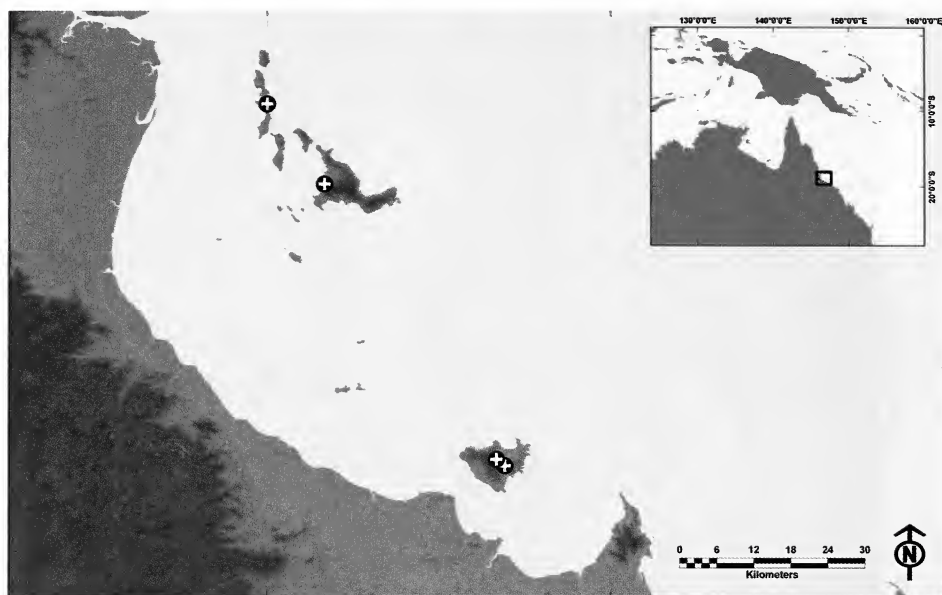


FIG. 31

Known localities of *Hormurus macrochela* n. spec. in northern Queensland, Australia, with topography indicated.

submedian carinae each with one or two spiniform granules subposteriorly, without spiniform granules medially or posteriorly. Segment II: Dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae without spiniform granules; ventro-submedian carinae each with one or two small spiniform granules medially, one or two subposteriorly, and none posteriorly. Segments III and IV: Posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral and ventro-submedian carinae weakly developed, sparsely granular, without spiniform granules. Segment V: Dorsal intercarinal surface sparsely granular; dorsolateral carinae obsolete; ventrolateral carinae weakly developed, posterior half comprising few spiniform granules becoming larger posteriorly; ventro-median carina weakly developed, comprising a sparse row of granules in anterior half, indistinct posteriorly; anal arch crenulate, comprising small denticles.

Telson: As long as or slightly longer than metasomal segment V (Fig. 28B); vesicle surfaces smooth.

Hemispermatoaphore (Figs 29-30): Distal lamina gently curved, approximately same length as basal part; distal crest absent; single laminar hook situated in basal third; basal extrusion absent; transverse ridge distinct, approximately aligned with base of laminar hook, merging with ental edge distal to laminar hook. Capsular lamella thin, folded proximally and unfolded distally to a flattened extremity (tip and base approximately the same width); longitudinal carina on dorsal surface absent; accessory hook

and accessory lobe absent; lamellar tip situated proximal to base of laminar hook, distal to tip of distal lobe. Distal lobe well developed, not hook-like, without accessory carina or crest, and with one or two large proximad-oriented accessory hooks on ental surface (Figs 29B-D, 30). Basal lobe well developed, spoon-shaped, merging with ental basal process; ectal edge without accessory fold, forming 135-150° angle with lamella; ental edge without accessory fold toward ectal part, forming 90° angle with lamella.

DESCRIPTION OF ADULT FEMALE: As for the ♂ except as follows.

Pedipalps: All segments shorter and more robust than in male (Figs 23B, D, 25A, F, K, 26B). Dentate margins of chela fingers linear or nearly so, i.e. without pronounced lobe and notch (Fig. 26B).

Genital operculum: Oval to semi-oval, wider than long, approximately same width as sternum (Fig. 27B); opercular sclerites partly fused, median suture distinct; posterior notch present, at least weakly developed.

Pectines: Short, distal edge not reaching distal edge of leg IV coxa (Fig. 27B). Pectinal tooth count 5-7; teeth short and curved, sensory papillae restricted to distal part.

Mesosoma: Intercarinal surfaces of post-tergites I-III smooth medially, granular laterally (Fig. 24B, F); intercarinal surfaces of IV-VI smooth or nearly so; intercarinal surfaces of VII granular posteriorly.

INTRASPECIFIC VARIATION: The pedipalps of larger males are proportionally longer than those of smaller males (positive allometry) (Monod, Harvey & Prendini, in preparation). Pectinal tooth counts vary from seven to nine in males and from five to seven in females. The distal lobe of the hemispermatophore usually bears one large hook on the ental edge, but two were observed in some specimens (Fig. 29A-C). This hook may be much more elongated, with a small posteriad-oriented excrescence (Fig. 29D) in some specimens.

REMARKS: Koch (1977) mentioned the large size of the pedipalp chela of specimens examined from Palm Island, but considered them conspecific with *L. waigiensis*. Volschenk *et al.* (2001) identified a specimen of this species from Magnetic Island as *L. waigiensis* based on the taxonomy current at the time.

DISTRIBUTION AND ECOLOGY: *Hormurus macrochela* is recorded from vine forests on three islands off the eastern coast of northern Queensland, between Ingham and Townsville (Fig. 31). Specimens were collected from narrow rock crevices and between stones near creeks in vine forest and rainforest. The habitat and habitus are consistent with the lithophilous ecomorphotype (Prendini, 2001).

CONSERVATION STATUS: The known populations of *H. macrochela* are situated on islands off the coast of northern Queensland, most of which are protected and part of two national parks (Orpheus Island National Park, Magnetic Island National Park). Therefore this species is not threatened by habitat destruction.

***Hormurus ochyroscapter* Monod, n. spec.**

Figs 32-37

Liocheles waigiensis: Koch, 1977 (misidentification, part): 169, 171, 172.

HOLOTYPE: QM-S17072; ♂; Australia, Queensland, Reedybrook [18°45'S, 144°38'E]; 2.VIII.1967; excavated from hole 6 inches deep, J. D. Brown.

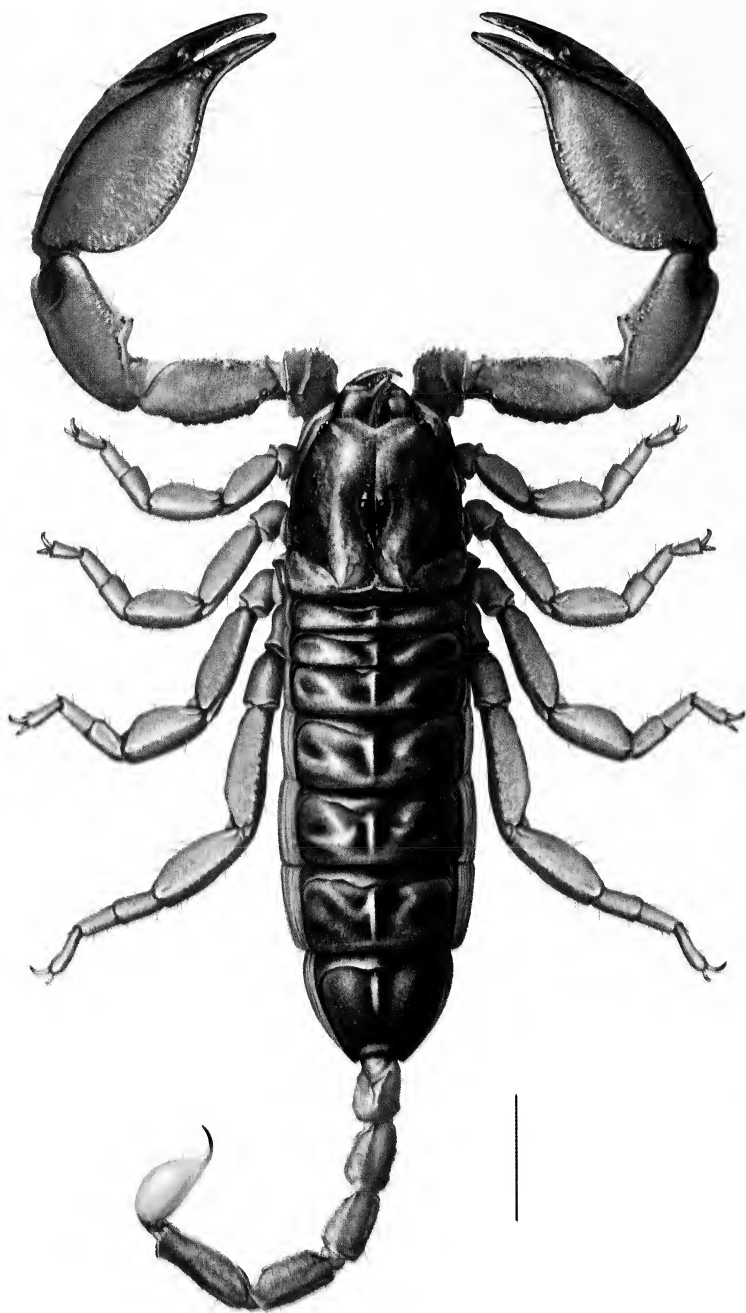


FIG. 32

Hormurus ochyroscapter n. spec., male, dorsal aspect, reconstruction based on scientific illustrations and photographs of live specimens. Scale, 5 mm.

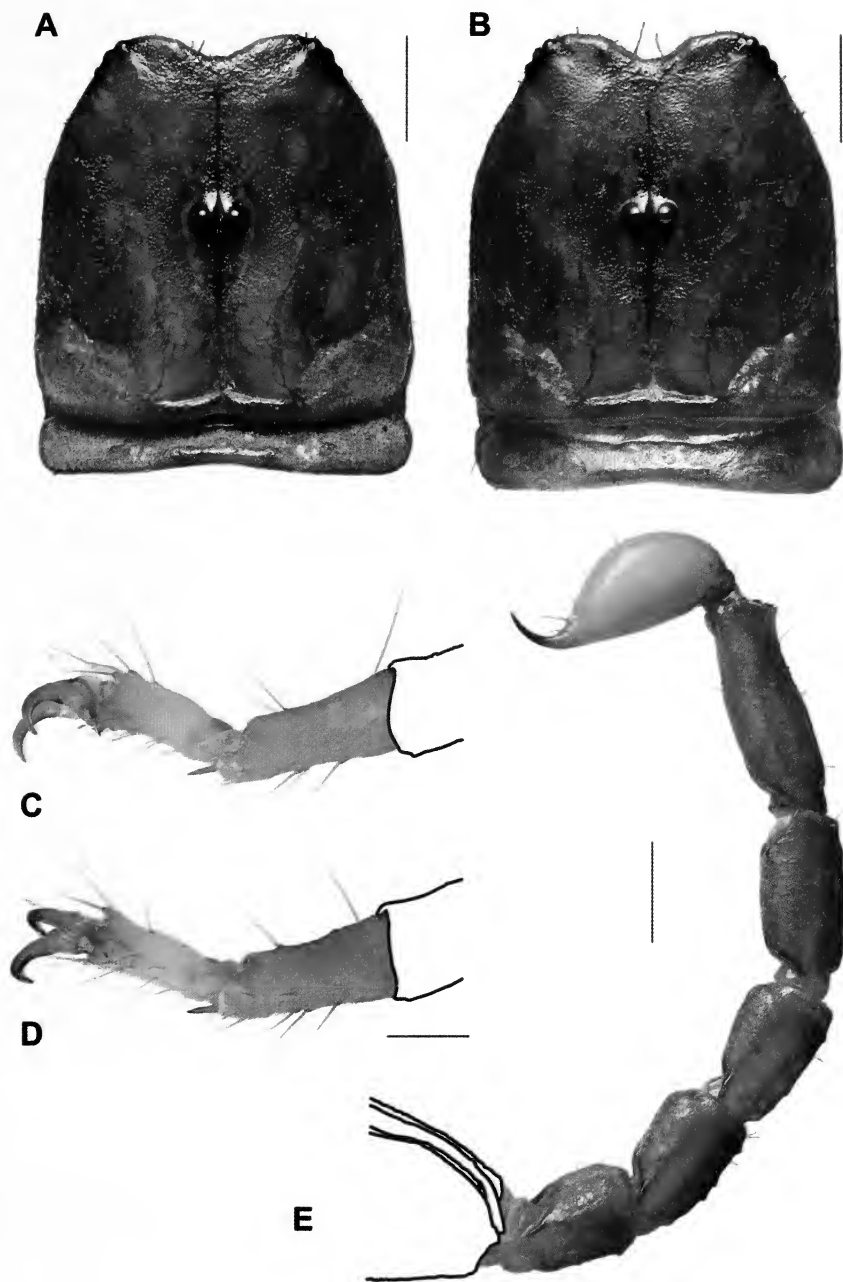


FIG. 33

Hormurus ochyroscapter n. spec., carapace and mesosomal tergite I (A, B), left tarsus IV, retro-lateral (C) and ventral (D) aspect, and metasoma and telson, lateral aspect (E). (A, C-E) Holotype male (QM-S17072). (B) Paratype female (QM-S17072). Scales, 2 mm (A, B, E), 1 mm (C, D).

PARATYPES: QM-S17072; 1 ♀, 2 imm.; same data as holotype.

OTHER MATERIAL: AM KS94922; 1 imm.; Almaden [17°20'S, 144°41'E], Chillagoe District; XI-XII.1925; W. D. Campbell.

ETYMOLOGY: The name *ochyroscapter* is constructed from the Greek words *ochyros* [strong, stout] and *skapter* [digger]. It is an invariable noun in apposition and refers to the robust pedipalps of this species that are typical of fossorial hormurids.

DIAGNOSIS: *Hormurus ochyroscapter* differs from other Australian hormurids as follows. The pedipalps of *H. ochyroscapter* are short and robust unlike those of other Australian species, which are more elongate. The digital carina of the pedipalp chela manus is smooth (costate) and the internomedian carina obsolete in *H. ochyroscapter*, whereas in other species the digital carina is granular and the internomedian carina distinct and at least weakly granular. The patellar prolateral process is weakly developed in *H. ochyroscapter*, its two spiniform granules fused medially but not developed into a prominent median spine as in other species. Pedipalp patellar trichobothrium *esb*₂ is situated closer to trichobothria *em*₁ and *em*₂ than to trichobothrium *esb*₁ in *H. ochyroscapter*, whereas in other species it is situated closer to *esb*₁. One pair of subposterior spiniform granules and one pair of weak medial spiniform granules, present on the ventro-submedian carinae of metasomal segment III in *H. ochyroscapter*, are absent in other species.

MEASUREMENTS: Holotype male (QM-S17072): Total body length, 47.0. Carapace length, 6.8, anterior width, 4.8, posterior width, 7.0. Pedipalp chela length, 13.2, manus width, 4.5, manus height, 3.1; movable finger length, 6.4; patella length, 7.2, width, 3.1; femur length, 6.2, width, 2.8. Metasomal segment I length, 2.9, width, 1.9; segment V length, 4.3, width, 1.5, height, 1.4; telson vesicle width, 1.6, vesicle height, 1.9. Paratype female (QM-S17072): Carapace length, 6.7, anterior width, 4.9, posterior width, 6.7. Pedipalp chela length, 11.6, manus width, 4.6, manus height, 3.2; movable finger length, 5.8; patella length, 6.1, width, 3.0; femur length, 5.0, width, 2.4. Metasomal segment I length, 2.8, width, 1.8. (measurements for metasomal segment V and telson were not recorded because the specimen is damaged).

DESCRIPTION OF ADULT MALE: *Colouration*: Dorsal surface of chelicera manus yellow to pale brown; darker infuscations on fingers (Fig. 32). Carapace pale to dark brown. Pedipalps yellow to pale brown; carinae and fingers reddish brown to black. Legs pale yellow. Tergites pale to dark brown, slightly paler than carapace. Coxapophyses, sternum, genital operculum, pectines and sternites pale yellow. Metasoma yellow to pale brown. Telson yellow; aculeus reddish black.

Cuticle: Non-granular surfaces of carapace, pedipalps and legs, mesosoma, and metasoma finely punctate.

Carapace: Anterior margin with shallow median notch (Fig. 33A). Anterior furcated sutures and sulci distinct. Median ocular tubercle situated anteromedially, slightly raised, small, occupying about 1/6-1/7 of carapace width; superciliary carinae present, smooth; median ocelli present, at least twice the size of lateral ocelli, separated by at least half the diameter of a median ocellus. Three pairs of lateral ocelli, equal in size, equidistant and adjacent to one another. Postocular carapace margin aspinose. Surfaces finely granular, at least sparsely so, except anteromedially, with frontal lobes smooth and fine granulation restricted to surfaces adjacent to anterior furcated and median longitudinal sulci.

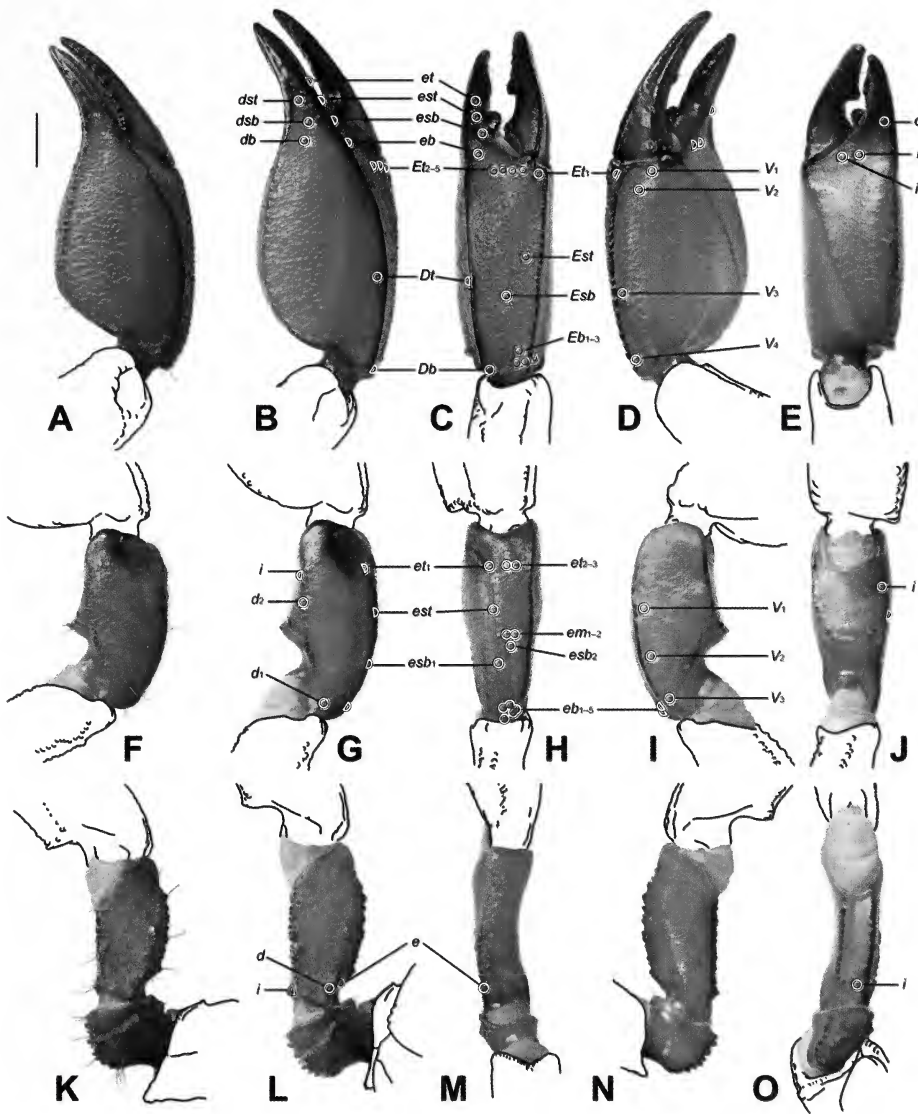


FIG. 34

Hormurus ochyroscaptor n. spec., pedipalp chela (A-E), patella (F-J), femur and trochanter (K-O), dorsal (A, B, F, G, K, L), retrolateral (C, H, M), ventral (D, I, N) and prolateral (E, J, O) aspect, illustrating trichobothrial pattern. (A, F, K) Paratype female (QM-S17072). (B-E, G-J, L-O) Holotype male (QM-S17072). Scale, 2 mm.

Chelicerae: Median and basal teeth of fixed finger fused into a bicusps. Dorsal margin of movable finger with four teeth (one subdistal and one basal); dorsal distal tooth smaller than ventral distal tooth; ventral margin smooth.

Pedipalps: All segments short and robust (Figs 32, 34B-E, G-J, L-O, 35A), with femur length less than carapace length. Chela almost asetose. Chela fingers: Dentate

margins of fixed and movable fingers linear (without lobes and notch) distally, with two rows of primary denticles, these rows fused to each other basally; larger primary denticles located at regular intervals in each row, accessory denticles absent. Fixed finger: Suprabasal lobe well developed, conical; suprabasal notch distinct and deep (Fig. 35A). Movable finger: Basal lobe absent or reduced to a few small spiniform granules; suprabasal lobe well developed, wider than high, gently rounded dorsally and lacking a sharp conical tooth, not overlapping fixed finger; suprabasal lobe and corresponding suprabasal notch in fixed finger contiguous, no proximal gap or at most a reduced gap evident when fingers closed. Pedipalp carinae: Femur (Fig. 34L-O): Dorsoexternal carina costate, usually more distinct in proximal half; dorsointernal carina distinct, more strongly developed than dorsoexternal carina; internomedian dorsal carina absent; internomedian ventral carina vestigial, comprising two large spiniform granules situated proximally and medially on segment; ventromedian carina obsolete; ventrointernal carina distinct. Patella (Fig. 34G-J): Prolateral process distinct but weakly developed, comprising two distinct spiniform granules fused medially but not developed into a prominent median spine; internodorsal and dorsomedian carina distinct; dorsoexternal carina obsolete; externomedian carina costate-granular; ventroexternal carina distinct, costate. Chela manus (Fig. 34B-E): Dorsal secondary carina obsolete; digital carina distinct, costate, more strongly developed than external secondary carina; external secondary carina absent or obsolete; ventroexternal carina granular or crenulate; ventromedian and ventrointernal carinae obsolete; internomedian carina obsolete. Surface macrosculpture: Femur (Fig. 34L-O): Dorsal intercarinal surface densely granular except distally; retrolateral intercarinal surface at least sparsely granular dorsally, smooth or nearly so ventrally; ventral intercarinal surface granular proximally, smooth distally; prolateral intercarinal surface smooth except for a sparsely granular zone proximally. Patella (Fig. 34G-J): Dorsal and retrolateral intercarinal surfaces granular or at least comprising a reticulated network of granules; ventral intercarinal surface sparsely granular, distal extremity smooth; prolateral intercarinal surface sparsely granular proximally, smooth or nearly so in distal half. Chela (Fig. 34B-E): Dorsal and retrolateral intercarinal surfaces of manus densely granular, comprising medium-sized granules; ventral intercarinal surface granular along pro- and retrolateral margins only, smooth medially; prolateral intercarinal surface sparsely granular, less so along ventral margin. Chela fingers granular, at least sparsely so in proximal half; *db*, *dsb* and *dst* trichobothria of fixed finger each situated in a smooth depression, surfaces around depressions granular (at least in proximal part of finger). Trichobothria: Pedipalps orthobothriotaxic, accessory trichobothria absent (Fig. 34B-E, G-J, L-O). Patella: *d*₂ distal to patellar process; five *eb* trichobothria arranged in two groups, *eb*₁ and *eb*₂₋₅; two *esb* trichobothria; two *em* trichobothria; *esb-em* series arranged in two groups, *esb*₂ and *esb*_{1/em}₁₋₂; one *est* trichobothrium; three *et* trichobothria; three *V* trichobothria. Chela manus with *Dt* situated in proximal third; *Eb*₃ situated close to *Eb*₁₋₂; *Esb* situated midway between *Eb* series and *Est*; *Est* situated at or near midpoint; four *V* trichobothria, with *V*₃ and *V*₄ separated. Chela fixed finger with *db* situated on dorsal surface; *eb*, *esb*, *est* and *et* equidistant (distance *esb-est* similar to distance *eb-esb*); *eb* situated at base of finger, behind point of articulation between fixed and movable fingers, aligned with *esb-et* axis; *esb* situated proximally on fixed finger, aligned with *est-et* axis; two *i* trichobothria.

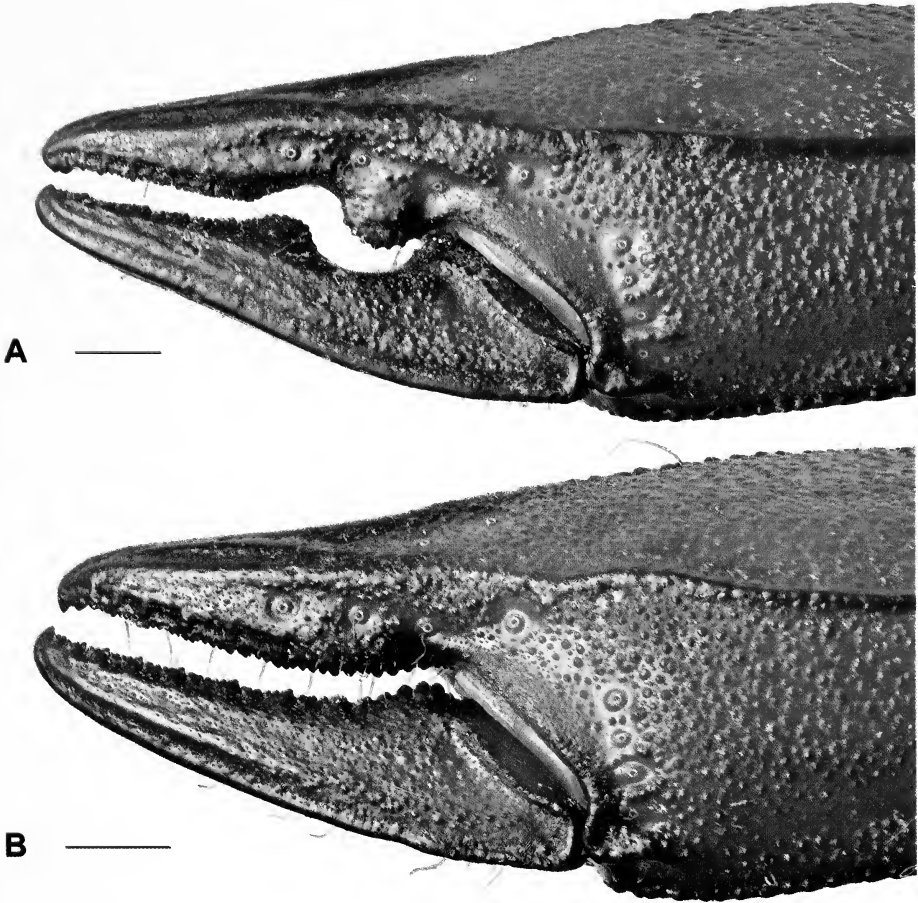


FIG. 35

Hormurus ochyroscapter n. spec., pedipalp chela, retrolateral aspect illustrating dentate margin of chela fingers. (A) Holotype male (QM-S17072). (B) Paratype female (QM-S17072). Scale, 1 mm.

Coxosternum: Leg III coxae without swelling or bulge anterodistally. Sternum equilateral pentagonal (Fig. 36A); anterior width slightly greater than posterior width; length less than or equal to posterior width.

Legs: Femora I-IV each with ventral surfaces bicarinate (proventral carinae less developed than retroventral carinae); IV with ventral carinae vestigial (only expressed distally) and indistinct, reduced to scattered granules. Retroventral margins of tibiae I and II without setiform macrosetae. Pro- and retroventral margins of basitarsi I-IV each with 4 setiform macrosetae. Telotarsi I-IV: Pro- and retroventral margins each with 4/4, 4/4, 4-5/5 and 5/5 setiform macrosetae, respectively (Fig. 33C, D); ventro-median row of spinules reduced to few spinules basally, terminal ventromedian spinules absent; dorsomedian lobe pronounced; laterodistal lobes truncate; ungues curved, shorter than telotarsus.

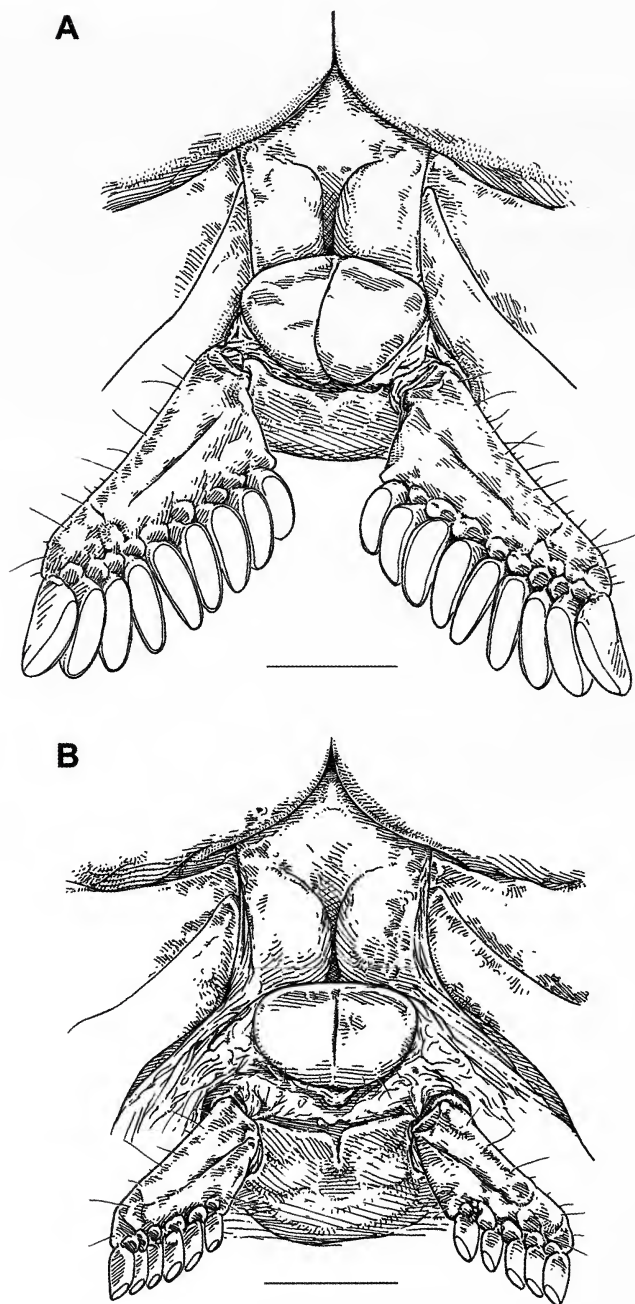


FIG. 36

Hormurus ochyroscapter n. spec., coxae of legs II-IV, sternum, genital operculum and pectines, ventral aspect. (A) Holotype male (QM-S17072). (B) Paratype female (QM-S17072). Scale, 1.5 mm.

Genital operculum: Composed of two subtriangular sclerites (Fig. 36A).

Pectines: Slightly elongated, distal edge reaching and surpassing distal edge of leg IV coxa (Fig. 36A); fulcra and three marginal lamellae present. Pectinal tooth count 8-9; teeth, long, straight, entirely covered with sensory papillae.

Mesosoma: Posterior margins of pre-tergites I-VII smooth. Posterior margins of post-tergites I-VII sublinear, without distinct prominence; I-VI each with lateral transverse sulci; intercarinal surfaces of I-VII finely granular, at least sparsely so in posterior half; intercarinal surfaces of III-VII uneven, with a distinct reticulated network of ridges and dimples. Respiratory stigmata (spiracles) of sternites IV-VI short, less than one third sternite width and crescent-shaped, with distinct curve; sternite VII acarinate.

Metasoma: Length similar to that of ♀, not flattened laterally (Fig. 33E), intercarinal surfaces sparsely granular. Segments I-IV each with median sulcus distinct and deep; segment V with sulcus shallow, especially in posterior half; dorso-submedian carinae absent or obsolete on all segments; dorsolateral, ventrolateral and ventro-submedian carinae distinct on at least some segments. Segment I: Width less than or equal to height; dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; lateral median carina distinct; ventro-submedian carinae each with one or two weakly developed spiniform granules medially, one or two subposteriorly, and none posteriorly. Segment II: Dorsomedian posterior spiniform granules weakly developed or absent; posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae without spiniform granules; ventro-submedian carinae each with one or two spiniform granules medially, 1-3 subposteriorly, and none posteriorly. Segments III and IV: Posterior spiniform granules of dorso-submedian carinae weakly developed or absent, not noticeably larger than preceding granules; ventrolateral carinae weakly developed, comprising a sparse row of granules, without larger spiniform granules; ventro-submedian carinae weakly developed, each with one weakly developed spiniform granule medially and one subposteriorly on III, and with several larger spiniform granules posteriorly on IV. Segment V: Dorsal intercarinal surface sparsely granular; dorsolateral carinae obsolete; ventrolateral carinae indistinct in anterior half, comprising few medium-sized spiniform granules in posterior half; ventromedian carina weakly developed, indistinct posteriorly; anal arch crenulate, comprising small denticles.

Telson: As long as or slightly longer than metasomal segment V (Fig. 33E); vesicle surfaces smooth.

Hemispermaphore: Distal lamina gently curved, slightly longer than basal part; distal crest absent; single laminar hook situated in basal third; basal extrusion absent; transverse ridge distinct, approximately aligned with base of laminar hook, merging with ental edge distal to laminar hook. Capsular lamella thin, folded proximally and unfolded distally to a flattened extremity (tip and base approximately the same width); longitudinal carina on dorsal surface absent to weak; accessory hook and accessory lobe absent; lamellar tip situated slightly proximal to base of laminar hook, distal to tip of distal lobe. Distal lobe well developed, not hook-like, without accessory

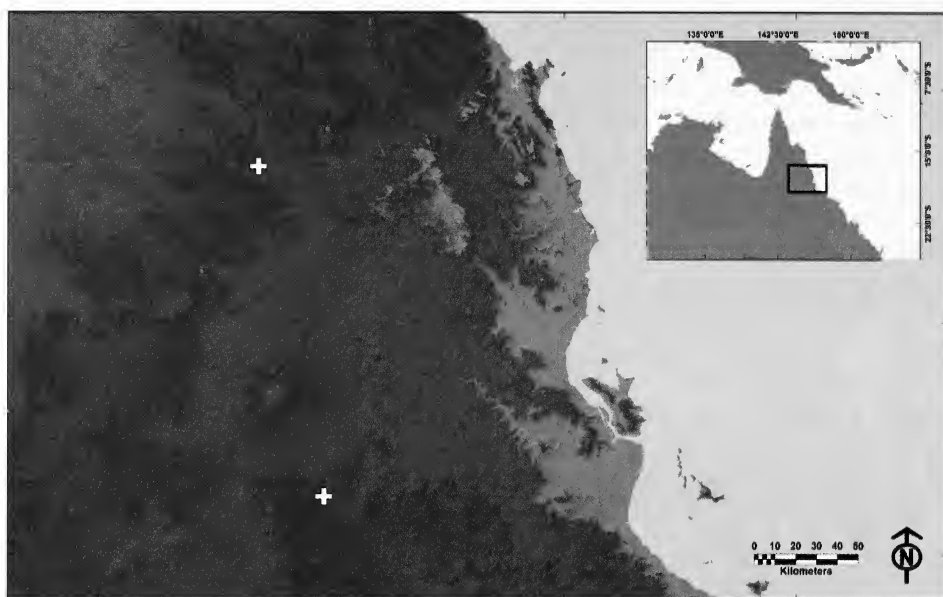


FIG. 37

Known localities of *Hormurs ochyroscapter* n. spec. in northern Queensland, Australia, with topography indicated.

carinae or crest, and with small proximad-oriented accessory hook on ental surface. Basal lobe well developed, spoon-shaped, merging with ental accessory lobe; ectal edge without accessory fold (no groove), forming 135-150° angle with lamella; ental edge without accessory fold toward ectal part, forming 90° angle with lamella.

DESCRIPTION OF ADULT FEMALE: As for the ♂ except as follows.

Pedipalps: Dentate margins of chela fingers linear or nearly so, i.e. without pronounced lobe and notch (Figs 34A, F, K, 35B).

Carapace: Medial surfaces slightly less granular than in male (Fig. 33B).

Genital operculum: Oval to semi-oval, wider than long, approximately same width as sternum (Fig. 36B); opercular sclerites partly fused, median suture distinct; posterior notch present, at least weakly developed.

Pectines: Short, distal edge not reaching distal edge of leg IV coxa (Fig. 36B). Pectinal tooth count 5-7; teeth short, curved, sensory papillae restricted to distal part.

Mesosoma: Intercarinal surfaces of post-tergites I-VII smooth or nearly so; intercarinal surfaces of III-VII even, reticulated network of ridges and dimples absent or obsolete.

INTRASPECIFIC VARIATION: Pectinal tooth counts vary from eight to nine in males, and from five to seven in females.

REMARKS: Koch (1977) mentioned the short pedipalps and unusual shape of the patellar process of specimens from Almaden and Reedybrook (constituting the examined material of *H. ochyroscapter*), but considered them conspecific with *L.*

waigiensis. Only one adult male and one adult female are known. Both are severely damaged, hence certain characters (female habitus, carapace and tergite macro-sculptures, metasoma of female, hemispermatophore) are not illustrated.

DISTRIBUTION: *Hormurus ochyroscapter* is recorded from open woodlands and savannah in the Charter Towers region and the Shire of Etheridge in Far North Queensland (Fig. 37).

ECOLOGY: *Hormurus ochyroscapter* was collected close to a waterbody in an inland savannah, a habitat similar to that of *H. ischnoryctes*. However, the climate at the type locality of *H. ochyroscapter* is drier than at the type locality of *H. ischnoryctes*, and there are no major rock formations that could potentially sustain humid conditions for extended periods. The known specimens of this fossorial species were excavated from ca 15 cm deep burrows. The habitat and habitus are consistent with the pelophilous ecomorphotype (Prendini, 2001).

CONSERVATION STATUS: This species is known from only two localities situated within the boundaries of privately owned cattle stations. The type specimens were collected in 1967 and no other specimens have been collected since. The first author visited Reedybrook in 2006 to obtain more specimens, but failed to find any during several days of intensive searching. The habitat there was severely disturbed by livestock, and this population of *H. ochyroscapter* may be extinct. Although there are no empirical data, it appears that population densities of burrowing scorpions in different parts of the world decline in areas where large numbers of hooved livestock are maintained, perhaps because their burrows are continuously damaged by the trampling of hooves, or due to a decrease in prey abundance and/or humidity associated with overgrazing of the vegetation (L. Monod and L. Prendini, personal observations). Based on the restricted distribution and degradation of its habitat, and despite the scarcity of data available on its distribution, ecology and abundance, it is recommended that *H. ochyroscapter* be placed on the IUCN Red List of endangered species (IUCN, 2001).

DISCUSSION

Most fossorial hormurid species belong to the genus *Cheloctonus* Pocock, 1892 from the semi-arid savannas of southern Africa. Several species of this genus construct vertical burrows with terminal chambers in open ground or against the sides of stones, in soils with high clay content, e.g. black turf (Newlands, 1972, 1978; Harington, 1978; Prendini, 2001, 2005b). Burrow entrances are slit-like in shape, and wider than high. Population densities of up to four individuals per square metre have been recorded for *Cheloctonus jonesii* Pocock, 1892 (Harington, 1978; L. Prendini, personal observation). Burrows of this species are 15–30 cm deep, with entrances 2–3 cm by 1–1.5 cm, and a small heap of excavated stones and soil particles is often present on one or both sides (Harington, 1978). The term ‘spoil’ is used in the present paper to designate these debris mounts instead of ‘tumulus’ originally proposed by Williams (1966). A spoil refers to the material (earth and rocks) removed during an excavation and is thus a more appropriate name than tumulus which refers to a mound of earth and stones raised over a grave.

Similar burrow architecture and population densities were observed for two species of *Liocheles* from Asia. In the woodlands and forests of India, *Liocheles*

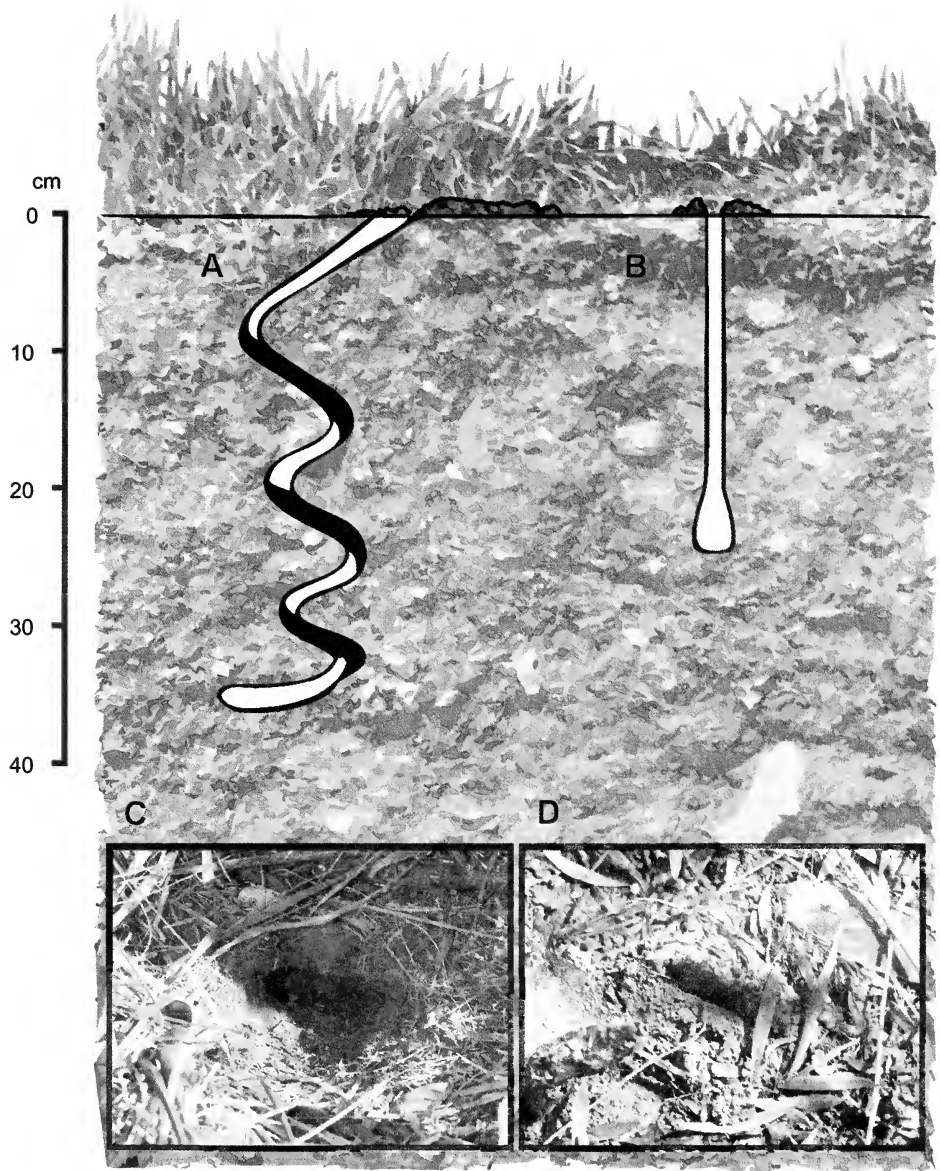


FIG. 38

Burrow architecture in urodacid and hormurid scorpions. (A) *Urodacus yaschenkoi* (Birula, 1903), diagrammatic cross-section of burrow (adapted from <http://www.thedailylink.com/thespiralburrow/>). (B) *Hormurus ischnoryctes* n. spec., diagrammatic cross-section of burrow. (C) *Urodacus* sp. from Mitchell River National Park, Western Australia, burrow entrance. (D) *Hormurus ischnoryctes* n. spec., burrow entrance. Scale in cm.

nigripes reportedly excavates vertical burrows 40–60 cm deep in sandy and stony soils with entrances 1.5–2.5 cm by 0.4–0.6 cm (Tilak, 1970). An undetermined fossorial *Liocheles* was recently collected in a Vietnamese forest (under closed canopy) by L. Prendini. The vertical burrows of this species were approximately 10 cm deep, and were constructed in open ground or along the side of a stone, along an earthen embankment comprising sandy-clay soil (L. Prendini, personal observation). A spoil was observed on one or both sides of the silt-like entrances, which were about 1 cm by 0.5 cm.

The burrows of *H. ischnoryctes* from the savanna of Queensland are vertical and about 15–30 cm deep, with a slit-like entrance and an enlarged terminal chamber (L. Monod, personal observation, Fig. 38B, D), much like in *C. jonesii*. The density of burrows in the only known population of this species appeared comparable to those of *C. jonesii* and *L. nigripes*, with numerous entrances in a small area. Burrows were predominantly located at the bases of trees and shrubs. Observations were made after unusually heavy rainfalls during the dry season. Most of the burrow entrances had recently excavated spoils on the sides, i. e. soil presumably carried outside the burrows by the scorpions after the rains subsided, as reported for *C. jonesii* (Harington, 1978).

According to the data labels, the known specimens of *H. ochyroscapter* were excavated from burrows approximately 15 cm deep. Unfortunately no other data concerning the burrow entrance or density are available for this species.

Burrowing behaviour appears to have evolved independently in three genera of Hormuridae, i.e. *Cheloctonus*, *Hormurus* and *Liocheles*. *Cheloctonus* is placed basal in the phylogeny of Hormuridae, and does not form a monophyletic group with *Hormurus* and *Liocheles* (Prendini, 2000). Additionally, *L. nigripes* does not form a monophyletic group with the two fossorial species of *Hormurus* (Monod, 2011; Monod & Prendini, in preparation), and it is presently unknown whether *H. ischnoryctes* and *H. ochyroscapter* are sister species. If the two fossorial *Hormurus* are not monophyletic, burrowing behaviour would have evolved independently on four occasions within the family.

Although there is no common ancestry for burrowing behaviour in Hormuridae, the burrow architecture is remarkably similar in all hormurid species in which it has been observed, suggesting a parallel evolution (sensu Powell, 2007). Moreover, burrow architecture is quite different in fossorial species of the closely related scorpionoid families Diplocentridae Karsch, 1880, Scorpionidae Latreille, 1802 and Urodacidae Pocock, 1893, the more distantly related Bothriuridae Simon, 1880, and the chactoid genera *Anuroctonus* Pocock, 1893 and *Hadrurus* Thorell, 1876. Most species in these taxa construct burrows at a 5–50° angle to the ground surface, rather than vertically, and often spiral down to an enlarged terminal chamber (Fig. 38A; Williams, 1966; Koch, 1978; Lamoral, 1979; Shorthouse & Marples, 1980; Shivashankar, 1992, 1994; Prendini *et al.*, 2003; Hembree *et al.*, 2012; L. Prendini, personal observation). The difference in burrow architecture is probably a consequence of the difference in the mechanics of burrow excavation. Fossorial hormurids are pedipalp burrowers that use the large, often rounded pedipalpal chelae to loosen the soil and carry it out of the burrow, whereas the other taxa are cheliceral burrowers that use their enlarged chelicerae to loosen the soil and then scrape it out of the burrow using the legs and/or

metasoma (Newlands, 1972; Eastwood, 1978; Harington, 1978; Prendini, 2001, 2005b; Hembree *et al.*, 2012).

Blackledge & Gillespie (2004) demonstrated that similar web architectures, termed "ethotypes", evolved independently in species of *Tetragnatha* Latreille, 1804 spiders from different Hawaiian islands, illustrating the high level of predictability that evolutionary diversification of complex behaviours may exhibit. Although less elaborate than web construction, burrow excavation is nonetheless a complex task, costly in time and energy (Shorthouse, 1971; Shorthouse & Marple, 1980; White, 2001), the expression of which appears to follow fixed patterns much like web construction in spiders. These observations in turn suggest that genetic pathways of burrowing behaviour, although not expressed, are conserved in hormurids that are not fossorial. Similar burrow architecture among distantly related hormurid genera suggests that burrowing behaviour did not evolve *de novo* in derived hormurid species, but is rather the expression of a basic behavioural trait suppressed in the common ancestor of Hormuridae. The suppression and re-expression of complex morphological structures or behaviours in distantly related lineages appears to be a more general trend than previously recognized (Wilkinson & Dodson, 1997; Whiting *et al.*, 2003; Bonduriansky, 2006) and points to the synergistic effect of similar selection pressures on highly conserved genetic pathways as a general mechanism for convergent evolution (Osorio & Bacon, 1994; Reichert & Boyan, 1997; Tomarev *et al.*, 1997; Ogura *et al.*, 2004; Emlen *et al.*, 2005).

ACKNOWLEDGEMENTS

This study was funded by a Graduate Student Fellowship from the AMNH, an Ernst Mayr grant from the Museum of Comparative Zoology, Harvard University, and a Synthesys grant to LM, as well as a National Science Foundation (NSF) grant (DEB 0910091) to LP and LM. Fieldwork in Australia in 2006 was funded by NSF grant EAR 0228699 and a grant from the Richard Lounsbery Foundation to LP, and in 2009 by a grant from the Australian Biological Resources Study to MH. Part of this study was carried out during the course of LM's Ph. D. thesis at the Graduate Center of the City University of New York (CUNY) and the AMNH. The authors thank the following persons for access to collections and/or for sending material on loan for study: Janet Beccaloni (NHML); Gavin Dally (NTM); Mike Gray and Graham Milledge (AM); Jacqueline Heurtault, Wilson Lourenço and Christine Rollard (MNH); Phil Lawless, Robert Raven and Owen Seeman (QM); Erich Volschenk and Julianne Waldo (WAM); for issuing collecting and export permits or helping with logistics on various expeditions: Graham Brown, Alain de Chambrier, Michelle Hatt, Michelle Ibbett, Anne O'Dea, Penny Scarpellino (Kakadu National Park); Jarrod Archibald (NTM); Ian Bryant, Rod Hancock, Peter Latch, Kerry Walsh, Carly Williams (EPA); Robert Raven (QM); for review and constructive comments on a draft of the manuscript: Peter Schwendinger and Erich Volschenk; for preparing the colour habitus reconstructions: Vladimir Timokhanov; for providing the photograph by Ian Oswald-Jacobs in Fig. 11A: Parks Australia; for technical assistance with SEM and optical equipment: Matthias Burger, Randy Mercurio, Gérard Monod, Tam Nguyen, Steve Thurston. LM

also wishes to express his gratitude to the following persons for assistance and hospitality during fieldwork: Graham and Janet Brown, Guillaume Courteheuse, Gwendolyn Romand, Julianne Waldock and Robin Wyss.

REFERENCES

- BANFAI, D. S. & BOWMAN, D. M. J. S. 2006. Forty years of lowland monsoon rainforest expansion in Kakadu National Park, Northern Australia. *Biological Conservation* 131: 553-565.
- BECKER, J. J., SANDWELL, D. T., SMITH, W. H. F., BRAUD, J., BINDER, B., DEPNER, J., FABRE, D., FACTOR, J., INGALLS, S., KIM, S.-H., LADNER, R., MARKS, K., NELSON, S., PHARAOH, A., TRIMMER, R., VON ROSENBERG, J., WALLACE, G. & WEATHERALL, P. 2009. Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Marine Geodesy* 32: 355-371. Available at http://topex.ucsd.edu/WWW_html/srtm30_plus.html (accessed 2011).
- BIRULA, A. A. 1903. Sur un nouveau genre et une nouvelle espèce de scorpion provenant d'Australie. *Annales du Musée Zoologique de l'Académie Impériale des Sciences de St-Petersbourg, Nouvelles* 8: 33 [in Russian, diagnosis in Latin].
- BLACKLEDGE, T. A. & GILLESPIE, R. G. 2004. Convergent evolution of behaviour in an adaptive radiation of Hawaiian web-building spiders. *Proceedings of the National Academy of Sciences* 101(46): 16228-16233.
- BONDURIANSKY, R. 2006. Convergent evolution of sexual shape dimorphism in Diptera. *Journal of Morphology* 267: 602-611.
- BOWMAN, D. M. J. S., WILSON, B. A. & MACDONOUGH, L. 1991. Monsoon forests in north-western Australia. I. Vegetation classification and the environmental control of tree species. *Journal of Biogeography* 18: 679-686.
- BULTITUDE, R. J., GARRAD, P. D., DONCHAK, P. J. T., DOMAGALA, J., CHAMPION, D. C., REES, I. D., MACKENZIE, D. E., WELLMAN, P., KNUSTON, J., FANNING, C. M., FORDHAM, B. G., GRIMES, K. G., OVERSBY, B. S., RIENKS, I. P., STEPHENSON, P. J., CHAPPELL, B. W., PAIN, C. F., WILFORD, J. R., RIGBY, J. F. & WOODBURY, M. J. 1997. Chapter 7. Cairns region. (pp. 225-325). In: BAIN, J. H. C. & DRAPER, J. J. (eds). North Queensland geology. *Australian Geological Survey Organisation Bulletin 240 / Queensland Department of Mines and Energy Queensland Geology* 9, 600 pp.
- CHAPMAN, A. D. & GRAFTON, O. 2008. Guide to best practices for generalising primary species-occurrence data, version 1.0. *Global Biodiversity Information Facility, Copenhagen*, 27 pp. Available at <http://www2.gbif.org/BPsensitivedata.pdf> (accessed 2011).
- COUZIUN, H. W. C. 1976. Functional anatomy of the walking-legs of Scorpionida with remarks on terminology and homologization of leg segments. *Netherlands Journal of Zoology* 26: 453-501.
- EASTWOOD, E. B. 1978. Notes on the scorpion fauna of the Cape. Part 4. The burrowing activities of some scorpionids and buthids (Arachnida, Scorpionida). *Annals of the South African Museum* 74: 249-255.
- EMERSON, D. W., MILLS, K. J., MIYAKAWA, K., HALLETT, M. S. & CAO, L. Q. 1992. Alligator Rivers Region Analogue Project, Final Report. Volume 4. Geophysics, petrophysics and structure. *Australian Nuclear Science and Technology Organisation (ANSTO), Sydney*, 125 pp.
- EMLÉN, D. J., HUNT, J. & SIMMONS, L. W. 2005. Evolution of sexual dimorphism and male dimorphism in the expression of beetle horns: phylogenetic evidence for modularity, evolutionary lability, and constraint. *American Naturalist* 166: 42-68.
- FAGE, L. 1933. Les scorpions de l'Indochine française, leur affinités, leur distribution géographique. *Annales de la Société entomologique de France (Paris)* 102: 25-34.
- FET, V. 2000. Family Ischnuridae Simon, 1879 (pp. 383-408). In: FET, V., SISSOM, W. D., LOWE, G. & BRAUNWALDER, M. E. (eds). Catalog of the scorpions of the world (1758-1998). *New York Entomological Society, New York*, 690 pp.

- FORDYCE, I. R., DUFF, G. A. & EAMUS, D. 1997. The water relations of *Allosyncarpia ternata* (Myrtaceae) at contrasting sites in the monsoonal tropics of northern Australia. *Australian Journal of Botany* 45: 259-274.
- GALLOWAY, R. W. 1976. Geomorphology of the Alligator rivers area (pp. 52-70). In: STORY, R., GALLOWAY, R. W., MCALPINE, J. R., ALDRICK, J. M. & WILLIAMS, M. A. J. (eds). Lands of the Alligator Rivers Area, Northern Territory. *Land Research Series* 38. CSIRO, Melbourne, 171 pp.
- GERVAIS, P. 1843. Les principaux résultats d'un travail sur la famille des scorpions. *Société Philomatique de Paris. Extraits des Procès-Verbaux des Séances* 5(7): 129-131.
- HADLEY, A. 2005. CombineZM. Available at <http://www.hadleyweb.pwp.blueyonder.co.uk/index.htm>.
- HADLEY, A. 2009. CombineZP. Available at <http://www.hadleyweb.pwp.blueyonder.co.uk/index.htm>.
- HARINGTON, A. 1978. Burrowing biology of the scorpion *Cheloctonus jonesii* Pocock (Scorpionida, Scorpionidae). *Journal of Arachnology* 5: 243-249.
- HEMBREE, D. I., JOHNSON, L. M. & TENWALDE, R. W. 2012. Neoichnology of the desert scorpion *Hadrurus arizonensis*: burrows to biogenic cross lamination. *Palaeontologica Electronica* 15(1): 10A, 34 pp.
- HOATSON, D., BLAKE, D., WYGRALAK, A., NEEDHAM, S., ALLEN, B., MILES, G., HAUSER, P. & OSWALD-JACOBS, I. 2000. Birth of Kakadu and Nitmiluk (pp. 31-43). In: HOATSON, D., BLAKE, D., WYGRALAK, A., NEEDHAM, S., ALLEN, B., MILES, G., HAUSER, P. & OSWALD-JACOBS, I. (eds). Kakadu and Nitmiluk National Parks, Northern Territory. A guide to the rocks, landforms, plants, animals, Aboriginal culture, and human impact. *Australian Geological Survey Organisation, Canberra*, 110 pp.
- HUXLEY, T. H. 1868. On the classification and distribution of the Alectoromorphae and Heteromorphae. *Proceedings of the Zoological Society of London* 36(1): 294-319.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (ICZN) 1999. International Code of Zoological Nomenclature - 4th Edition - *The International Trust for Zoological Nomenclature, The Natural History Museum, London*, 306 pp.
- INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE (IUCN) 2001. IUCN Red List categories and criteria. Version 3.1. *IUCN Species Survival Commission, IUCN, Gland, Switzerland / Cambridge, UK*. Available at http://www.iucnredlist.org/static/categories_criteria.
- JARVIS, A., REUTER, H. I., NELSON, A. & GUEVARA, E. 2008. Hole-filled seamless SRTM data V4. *International Centre for Tropical Agriculture (CIAT)*. Available at <http://srtm.csi.cgiar.org> (accessed 2011).
- JOHNSON, D. 2004. The geology of Australia. *Cambridge University Press, Cambridge*, 276 pp.
- KARSCH, F. 1880. Arachnologische Blätter. X. Scorpionologische Fragmente. *Zeitschrift für die Gesellschaft der Naturwissenschaften* 53: 404-409.
- KOCH, L. E. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. *Records of the Western Australian Museum* 5(2): 83-367.
- KOCH, L. E. 1978. A comparative study of the structure, function and adaptation to different habitats of burrows in the scorpion genus *Urodacus* (Scorpionida, Scorpionidae). *Records of the Western Australian Museum* 6(2): 119-146.
- KOVAŘÍK, F. 1998. Štíři (Scorpions). *Nakladatelství Madagaskar, Jihlava*, 175 pp.
- LAMORAL, B. H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* 23(3): 497-784.
- LATREILLE, P. A. 1802. Scorpionides (pp. 46-47). In: Histoire naturelle, générale et particulière, des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc et Buffon, et rédigée par C. S. Sonnini. Tome III. *Imprimerie F. Dufart, Paris*, 467 pp.
- LATREILLE, P. A. 1804. Tableau méthodique des insectes. *Nouveau Dictionnaire d'Histoire Naturelle, Paris* 21: 129-295.
- LAURIE, M. 1896. Further notes on the anatomy and development of scorpions, and their bearing on the classification of the order. *Annals and Magazine of Natural History* (6) 18: 9-133.

- LAWRENCE, R. F. 1954. Fluorescence in Arthropoda. *Journal of the Entomological Society of South Africa* 17: 167-170.
- LOCKET, A. 1995. A new ischnurid scorpion from the Northern Territory, Australia. *Records of the Western Australian Museum* supplement 52: 191-198.
- LOCKET, A. 1997. *Liocheles extensa*, a replacement name for *Liocheles longimanus* Locket, 1995 (Scorpiones: Ischnuridae). *Records of the Western Australian Museum* 18: 331.
- MONOD, L. 2000. Révision systématique du genre *Liocheles* (Ischnuridae, Scorpiones). *M.Sc. thesis, University of Geneva, Switzerland*, 143 pp.
- MONOD, L. 2011. The Liochelidae Fet & Bechly, 2001 (Scorpiones) of the Indo-Pacific region: Systematics and biogeography. *Ph.D. thesis, City University of New York*, 2 volumes, 848 pp.
- MONOD, L. & VOLSCHENK, E. S. 2004. *Liocheles litodactylus* (Scorpiones: Liochelidae): An unusual new *Liocheles* species from the Australian Wet Tropics (Queensland). *Memoirs of the Queensland Museum* 49(2): 675-690.
- MONTREAL PROCESS IMPLEMENTATION GROUP FOR AUSTRALIA (MPIGA) 2008. Australia's state of the forests report 2008. *Bureau of Rural Sciences, Canberra*, 250 pp.
- NAVIDPOUR, S. & LOWE, G. 2009. Revised diagnosis and redescription of *Apistobuthus susanae* (Scorpiones, Buthidae). *Journal of Arachnology* 37: 45-59.
- NEWLANDS, G. 1972. Ecological adaptations of Kruger National Park scorpionids (Arachnida: Scorpiones). *Koedoe* 15: 37-48.
- NEWLANDS, G. 1978. Arachnida (except Acari) (pp. 677-684). In: WERGER, M. J. A. (ed.). *Biogeography and Ecology of southern Africa*, volume 2. *W. Junk, The Hague*, 777 pp.
- NOWAK, A., LIS, P. & RADZIEJEWSKA, T. 2008. Sonication as an aid in cleaning cladoceran remains extracted from sediment cores. *Journal of Paleolimnology* 39: 133-136.
- OGURA, A., IKEO, K. & GOJOBORI, T. 2004. Comparative analysis of gene expression for convergent evolution of camera eye between octopus and human. *Genome Research* 14: 1555-1561.
- OJANGUREN-AFFILASTRO, A. A., AGUSTO, P., PIZARRO-ARAYA, J. & MATTONI, C. I. 2007. Two new scorpion species of the genus *Brachistosternus* (Scorpiones: Bothriuridae) from northern Chile. *Zootaxa* 1623: 55-68.
- OJANGUREN-AFFILASTRO, A. A., FERNÁNDEZ CAMPÓN, F., LAGOS SILNIK, S. & MATTONI, C. I. 2009. The genus *Oroborthriurus* Maury in central Argentina with description of a new species from El Nevado mountain chain in Mendoza Province (Scorpiones: Bothriuridae). *Zootaxa* 2209: 28-42.
- OSORIO, D. & BACON, J. P. 1994. A good eye for arthropod evolution. *Bioessays* 16: 419-424.
- PAVAN, M. 1954a. Presenza e distribuzione di una sostanza fluorescente nel tegumento degli scorpioni. *Bolletino della Società Italiana di Biologia Sperimentale* 30: 801-803.
- PAVAN, M. 1954b. Primi dati per la caratterizzazione della sostanza fluorescente nel tegumento degli scorpioni. *Bolletino della Società Italiana di Biologia Sperimentale* 30: 803-805.
- PAVAN, M. 1954c. Studi sugli scorpioni. I. Una nuova caratteristica tipica del tegumento degli scorpioni. *Italian Journal of Zoology* 21: 283-291.
- PAVAN, M. & VACHON, M. 1954. Sur l'existence d'une substance fluorescente dans les téguments de scorpions (Arachnides). *Comptes Rendus de l'Académie des Sciences (Paris)* 239: 1700-1702.
- POCOCK, R. I. 1892. Description of two new genera of scorpions, with notes on some species of *Palamneus*. *Annals and Magazine of Natural History* (6) 9: 38-49.
- POCOCK, R. I. 1893. Notes on the classification of scorpions, followed by some observations on synonymy, with descriptions of new genera and species. *Annals and Magazine of Natural History* (6) 12: 303-330.
- POCOCK, R. I. 1897. Description of some new species of scorpions from India. *Journal of the Bombay Natural History Society* 11: 102-117.
- POWELL, R. 2007. Is convergence more than an analogy? Homoplasy and its implications for macroevolution predictability. *Biology and Philosophy* 22: 565-578.

- PRENDINI, L. 2000. Phylogeny and classification of the superfamily Scorpionoidea Latreille, 1802 (Chelicerata, Scorpiones): an exemplar approach. *Cladistics* 16: 1-78.
- PRENDINI, L. 2001. Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited (pp. 113-138). In: FET, V. & SELDEN, P. A. (eds). *Scorpions 2001. In memoriam Gary A. Polis. British Arachnological Society, Burnham Beeches, Bucks*, 404 pp.
- PRENDINI, L. 2003a. A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence. *Systematic Entomology* 28: 149-172.
- PRENDINI, L. 2003b. Discovery of the male of *Parabuthus muelleri*, and implications for the phylogeny of *Parabuthus* (Scorpiones: Buthidae). *American Museum Novitates* 3408: 1-24.
- PRENDINI, L. 2004. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): Revisions to the taxonomy and key to the species. *Journal of Arachnology* 32: 109-186.
- PRENDINI, L. 2005a. On *Hadogenes angolensis* Lourenço, 1999 syn. n. (Scorpiones, Liochelidae), with a redescription of *H. taeniurus* (Thorell, 1876). *Revue suisse de Zoologie* 112(2): 371-399.
- PRENDINI, L. 2005b. Scorpion diversity and distribution in southern Africa: Pattern and process (pp. 25-68). In: HUBER, B. A., SINCLAIR, B. J. & LAMPE, K.-H. (eds). *African Bio-diversity: molecules, organisms, ecosystems. Proceedings of the 5th International Symposium on Tropical Biology; Museum Alexander Koenig, Bonn; Springer Verlag, New York*, 443 pp.
- PRENDINI, L. 2006. New South African flat rock scorpions (Liochelidae: *Hadogenes*). *American Museum Novitates* 3502: 1-32.
- PRENDINI, L., CROWE, T. M. & WHEELER, W. C. 2003. Systematics and biogeography of the family Scorpionidae (Chelicerata: Scorpiones), with a discussion on phylogenetic methods. *Invertebrate Systematics* 17: 185-259.
- PRENDINI, L., VOLSCHENK, E. S., MAALIKI, S. & GROMOV, A. V. 2006. A 'living fossil' from Central Asia: the morphology of *Pseudochactas ovchinnikovi* Gromov, 1998 (Scorpiones: Pseudochactidae), with comments on its phylogenetic position. *Zoologischer Anzeiger* 245: 211-248.
- PRICE, O., WOINARSKI, J. C. Z., LIDDLE, D. L. & RUSSELL-SMITH, J. 1995. Patterns of species composition and reserve design for a fragmented estate: monsoon rainforests in the Northern Territory, Australia. *Biological Conservation* 74: 9-19.
- REICHERT, H. & BOYAN, G. 1997. Building a brain: development insights in insects. *Trends in Neurosciences* 20: 258-264.
- RUSSELL-SMITH, J. 1991. Classification, species richness, and environmental relations of monsoon rainforest vegetation in the Northern Territory, Australia. *Journal of Vegetation Science* 2: 259-278.
- RUSSELL-SMITH, J. & BOWMAN, D. M. J. S. 1992. Conservation of monsoon rainforest isolates in the Northern Territory, Australia. *Biological Conservation* 50: 51-63.
- RUSSELL-SMITH, J., MACKENZIE, N. L. & WOINARSKI, J. C. Z. 1992. Conserving vulnerable habitat in northern and northwestern Australia: the rainforest archipelago (pp. 63-68). In: MOFFAT, I. & WEBB, A. (eds). *Conservation and development issues in north Australia. North Australia Research Unit, Darwin*, 277 pp.
- SHIVASHANKAR, T. 1992. The importance of burrowing for the scorpion *Heterometrus fulvipes* Koch (Arachnida). *Journal of Soil Biology and Ecology* 12: 134-138.
- SHIVASHANKAR, T. 1994. Advanced sub social behaviour in the scorpion *Heterometrus fulvipes* Brunner (Arachnida). *Journal of Biosciences* 19(1): 81-90.
- SHORTHOUSE, D. J. 1971. Studies on the biology and energetics of the scorpion *Urodacus yaschenkoi* (Birula, 1904). *Ph.D. thesis, Australian National University, Canberra*, 163 pp.

- SHORTHOUSE, D. J. & MARPLES, T. G. 1980. Observations on the burrow and associated behaviour of the arid-zone scorpion *Urodacus yaschenko* (Birula). *Australian Journal of Zoology* 28: 581-590.
- SIMON, E. 1880. Etudes arachnologiques. 12ème mémoire. XVIII. Descriptions de genres et espèces de l'ordre des scorpions. *Annales de la Société Entomologiques de France* (5) 10: 377-398.
- SNELLING, A. A. 1992. Alligator Rivers Region Analogue Project, Final Report. Volume 2. Geologic setting. *Australian Nuclear Science and Technology Organisation (ANSTO)*, Sydney, 118 pp.
- STACHEL, S. J., STOCKWELL, S. A. & VAN VRANKEN, D. L. 1999. The fluorescence of scorpions and cataractogenesis. *Chemistry & Biology* 6: 531-539.
- STAHNKE, H. L. 1970. Scorpion nomenclature and mensuration. *Entomological News* 81: 297-316.
- STAHNKE, H. L. 1972. UV light, a useful field tool. *Bioscience* 22: 604-607.
- STOCKWELL, S. A. 1989. Revision of the phylogeny and higher classification of scorpions (Chelicerata). *Ph.D. thesis, University of California, Berkeley*, 413 pp.
- SUNDEVALL, C. J. 1833. Conspectus Arachnidum. *Sveno Hardin et Erico T. Hammergren, Vermlandis, London-Göteborg*, 39 pp.
- THORELL, T. 1876. On the classification of scorpions. *Annals and Magazine of Natural History* 4(17): 1-15.
- TILAK, R. 1970. On an interesting observation on the living habit of *Hormurus nigripes* Pocock (Ischnuridae: Arachnida). *Science and Culture* 36: 174-176.
- TOMAREV, S. I., CALLAERTS, P., KOS, L., ZINOVIEVA, R., HALDER, G., GEHRING, W. & PIATIGORSKY, J. 1997. Squid Pax-6 and eye development. *Proceedings of the National Academy of Sciences, USA* 94: 2421-2426.
- VACHON, M. 1956. Sur des nouveaux caractères familiaux et génériques chez les scorpions (pp. 471-474). In: *Proceedings of the XIV International Congress of Zoology, Copenhagen, 5-12 August 1953. Danish Science Press, Copenhagen*, 567 pp.
- VACHON, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle (Paris)* (Ser. 2) 35: 161-166.
- VACHON, M. 1974. Etude des caractères utilisés pour classer les familles et les genres de scorpions (Arachnides). 1. La trichobothriotaxie chez les scorpions. *Bulletin du Muséum National d'Histoire Naturelle (Paris)* (Ser. 3) 140: 857-958.
- VIGNOLI, V. & PRENDINI, L. 2008. A new species of *Akentrobuthus* Lamoral, 1976 (Scorpiones: Buthidae) from the Republic of Benin (Western Africa). *Journal of Afrotropical Zoology* 4: 61-70.
- VIGNOLI, V. & PRENDINI, L. 2009. Systematic revision of the troglomorphic North American scorpion family Typhlochactidae (Scorpiones: Chactioidea). *Bulletin of the American Museum of Natural History* 326: 1-94.
- VOLSCHENK, E. S. 2002. Systematic revision of the scorpion genera in the family Buthidae. *Ph.D. thesis, Curtin University of Technology*, 224 pp.
- VOLSCHENK, E. S. 2005. A new technique for examining surface morphosculpture of scorpions. *Journal of Arachnology* 33: 820-825.
- VOLSCHENK, E. S., LOCKET, N. A. & HARVEY, M. S. 2001. First record of a troglotibic ischnurid scorpion from Australasia (Scorpiones: Ischnuridae) (pp. 161-170). In: FET, V. & SELDEN, P. A. (eds). *Scorpions 2001. In memoriam Gary A. Polis. British Arachnological Society, Burnham Beeches, Bucks*, 404 pp.
- WERNER, F. 1939. Ueber einige Scorpione aus dem Museum Alexander Koenig. *Festschrift zum 60. Geburtstag von Professor Dr. Embrik Strand (Riga)* 5: 361-362.
- WHITE, C. R. 2001. The energetics of burrow excavation by the inland robust scorpion, *Urodacus yaschenko* (Birula, 1903). *Australian Journal of Zoology* 49: 663-674.

- WHITING, M. F., BRADLER, S. & MAXWELL, T. 2003. Loss and recovery of wings in stick insects. *Nature* 421: 264-267.
- WILKINSON, G. S. & DODSON, G. N. 1997. Function and evolution of antlers and eye stalks in flies. (pp. 310-328). In: CHOE, J. C. & CRESPI, B. J. (eds). The evolution of mating systems in insects and arachnids. *Cambridge University Press, Cambridge*, 400 pp.
- WILLIAMS, S. C. 1966. Burrowing activities of the scorpion *Anuroctonus phaeodactylus* (Wood) (Scorpionida: Vejovidae). *Proceedings of the California Academy of Sciences* 34: 419-428.
- WYRWOLL, K.-H. 1992. Alligator Rivers Region Analogue Project, Final Report. Volume 3. Geomorphology and palaeoclimatic history. *Australian Nuclear Science and Technology Organisation (ANSTO), Sydney*, 93 pp.
- WITHNALL, I. W., DRAPER, J. J., MACKENZIE, D. E., KNUSTON, J., BLEWETT, R. S., HUTTON, L. J., BULTITUDE, R. J., WELLMAN, P., MACCONACHIE, B. A., BAIN, J. H. C., DONCHAK, P. J. T., LANG, S. C., DOMALGA, J., SYMONDS, P. A. & RIENKS, I. P. 1997. Chapter 14. Review of geological provinces and basins of north Queensland (pp. 449-527). In: BAIN, J. H. C. & DRAPER, J. J. (eds). North Queensland geology. *Australian Geological Survey Organisation Bulletin 240 / Queensland Department of Mines and Energy Queensland Geology* 9, 600 pp.

REVUE SUISSE DE ZOOLOGIE

Tome 120 — Fascicule 2

	Pages
SMALES, L. R. Acanthocephala including the descriptions of new species of <i>Centrorhynchus</i> (Centrorhynchidae) and the redescription of <i>Lueheia inscripta</i> (Westrumb, 1821) (Plagiorhynchidae) from birds from Paraguay South America	175-202
HOLLIER, J. An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève, Part 4: The Acridomorpha excluding the superfamily Acridoidea	203-219
HOLLIER, J. The Embioptera (Insecta) described by Henri de Saussure . . .	221-227
HERTACH, T. & NAGEL, P. Cicadas in Switzerland: a scientific overview of the historic and current knowledge of a popular taxon (Hemiptera: Cicadidae)	229-269
BESUCHET, C., CUCCODORO, G. & SABELLA, G. On the genera <i>Acanthobythus</i> Normand, 1930 and <i>Ceratobythus</i> Normand 1932 (Coleoptera: Staphylinidae: Pselaphinae)	271-280
MONOD, L., HARVEY, M. S. & PRENDINI, L. Stenotopic <i>Hormurus</i> Thorell, 1876 scorpions from the monsoon ecosystems of northern Australia, with a discussion on the evolution of burrowing behaviour in Hormuridae Laurie, 1896	281-346

REVUE SUISSE DE ZOOLOGIE

Volume 120 — Number 2

Pages

SMALES, L. R. <i>Acanthocephala</i> including the descriptions of new species of <i>Centrorhynchus</i> (Centrorhynchidae) and the redescription of <i>Lueheia inscripta</i> (Westrumb, 1821) (Plagiorhynchidae) from birds from Paraguay South America	175-202
HOLLIER, J. An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève, Part 4: The Acridomorpha excluding the superfamily Acridoidea	203-219
HOLLIER, J. The Embioptera (Insecta) described by Henri de Saussure . . .	221-227
HERTACH, T. & NAGEL, P. Cicadas in Switzerland: a scientific overview of the historic and current knowledge of a popular taxon (Hemiptera: Cicadidae)	229-269
BESUCHET, C., CUCCODORO, G. & SABELLA, G. On the genera <i>Acanthobythus</i> Normand, 1930 and <i>Ceratobythus</i> Normand 1932 (Coleoptera: Staphylinidae: Pselaphinae)	271-280
MONOD, L., HARVEY, M. S. & PRENDINI, L. Stenotopic <i>Hormurus</i> Thorell, 1876 scorpions from the monsoon ecosystems of northern Australia, with a discussion on the evolution of burrowing behaviour in Hormuridae Laurie, 1896	281-346

Indexed in CURRENT CONTENTS, SCIENCE CITATION INDEX

PUBLICATIONS DU MUSEUM D'HISTOIRE NATURELLE DE GENÈVE

CATALOGUE DES INVERTEBRES DE LA SUISSE, N ^{os} 1-17 (1908-1926)	série	Fr.	285.—
(prix des fascicules sur demande)			
REVUE DE PALÉOBIOLOGIE	Echange ou par fascicule	Fr.	35.—
LE RHINOLOPHE (Bulletin du centre d'étude des chauves-souris)	par fascicule	Fr.	35.—
THE EUROPEAN PROTURA: THEIR TAXONOMY, ECOLOGY AND DISTRIBUTION, WITH KEYS FOR DETERMINATION			
J. NOSEK, 345 p., 1973		Fr.	30.—
CLASSIFICATION OF THE DIPLOPODA			
R. L. HOFFMAN, 237 p., 1979		Fr.	30.—
LES OISEAUX NICHEURS DU CANTON DE GENÈVE			
P. GÉROUDET, C. GÜEX & M. MAIRE			
351 p., nombreuses cartes et figures, 1983		Fr.	45.—
CATALOGUE COMMENTÉ DES TYPES D'ECHINODERMES ACTUELS CONSERVÉS DANS LES COLLECTIONS NATIONALES SUISSES, SUIVI D'UNE NOTICE SUR LA CONTRIBUTION DE LOUIS AGASSIZ À LA CONNAISSANCE DES ECHINODERMES ACTUELS			
M. JANGOUX, 67 p., 1985		Fr.	15.—
RADULAS DE GASTÉROPODES LITTORAUX DE LA MANCHE (COTENTIN-BAIE DE SEINE, FRANCE)			
Y. FINET, J. WÜEST & K. MAREDA, 62 p., 1991		Fr.	10.—
GASTROPODS OF THE CHANNEL AND ATLANTIC OCEAN: SHELLS AND RADULAS			
Y. FINET, J. WÜEST & K. MAREDA, 1992		Fr.	30.—
O. SCHMIDT SPONGE CATALOGUE			
R. DESQUEYROUX-FAUNDEZ & S.M. STONE, 190 p., 1992		Fr.	40.—
ATLAS DE RÉPARTITION DES AMPHIBIENS ET REPTILES DU CANTON DE GENÈVE			
A. KELLER, V. AELLEN & V. MAHNERT, 48 p., 1993		Fr.	15.—
THE MARINE MOLLUSKS OF THE GALAPAGOS ISLANDS: A DOCUMENTED FAUNAL LIST			
Y. FINET, 180 p., 1995		Fr.	30.—
NOTICE SUR LES COLLECTIONS MALACOLOGIQUES DU MUSEUM D'HISTOIRE NATURELLE DE GENEVE			
J.-C. CAILLIEZ, 49 p., 1995		Fr.	22.—
PROCEEDINGS OF THE XIII th INTERNATIONAL CONGRESS OF ARACHNOLOGY, Geneva 1995 (ed. V. MAHNERT), 720 p. (2 vol.), 1996			
		Fr.	160.—

INSTRUMENTA BIODIVERSITATIS

CATALOGUE OF THE SCAPHIDIINAE (COLEOPTERA: STAPHYLINIDAE) (<i>Instrumenta Biodiversitatis</i> I), I. LÖBL, xii + 190 p., 1997	Fr. 50.—
CATALOGUE SYNONYMIQUE ET GEOGRAPHIQUE DES SYRPHIDAE (DIPTERA) DE LA REGION AFROTROPICALE (<i>Instrumenta Biodiversitatis</i> II), H. G. DIRICKX, x + 187 p., 1998	Fr. 50.—
A REVISION OF THE CORYLOPHIDAE (COLEOPTERA) OF THE WEST PALAEARCTIC REGION (<i>Instrumenta Biodiversitatis</i> III), S. BOWESTEAD, 203 p., 1999	Fr. 60.—
THE HERPETOFAUNA OF SOUTHERN YEMEN AND THE SOKOTRA ARCHIPELAGO (<i>Instrumenta Biodiversitatis</i> IV), B. SCHÄTTI & A. DESVOIGNES, 178 p., 1999	Fr. 70.—
PSOCOPTERA (INSECTA): WORLD CATALOGUE AND BIBLIOGRAPHY (<i>Instrumenta Biodiversitatis</i> V), C. LIENHARD & C. N. SMITHERS, xli + 745 p., 2002	Fr. 180.—
REVISION DER PALÄARKTISCHEN ARTEN DER GATTUNG <i>BRACHYGLUTA</i> THOMSON, 1859 (COLEOPTERA, STAPHYLINIDAE) (1. Teil) (<i>Instrumenta Biodiversitatis</i> VI), G. SABELLA, CH. BÜCKLE, V. BRACHAT & C. BESUCHET, vi + 283 p., 2004	Fr. 100.—
PHYLOGENY, TAXONOMY, AND BIOLOGY OF TEPHRITOID FLIES (DIPTERA, TEPHRITOIDEA) Proceedings of the "3rd Tephritoid Taxonomist's Meeting, Geneva, 19.-24. July 2004" (<i>Instrumenta Biodiversitatis</i> VII). B. MERZ, vi + 274 p., 2006	Fr. 100.—
LISTE ANNOTÉE DES INSECTES (INSECTA) DU CANTON DE GENÈVE (<i>Instrumenta Biodiversitatis</i> VIII). (ed. B. MERZ), 532 p., 2012	Fr. 85.—

Revue suisse de Zoologie: Instructions for Authors

The *Revue suisse de Zoologie* publishes original results of zoological systematics and related fields. Priority is given to contribution submitted by members of the Swiss Zoological Society or studies presenting results based on collections of Seiss museums. Contributions from other authors may be accepted as space permits.

Submission of a manuscript implies that it has been approved by all authors, that it reports their unpublished work and that it is not being considered for publication elsewhere. A financial contribution may be asked from the authors for the impression of colour plates. All manuscripts are refereed by experts.

In order to facilitate publication and avoid delays authors should follow the *Instructions to Authors* and refer to a current issue of the RSZ or our web-pages for acceptable style and format. Papers may be written in French, German, Italian and English. Authors and writing in their native language should pay particular attention to the linguistic quality of the text.

Manuscripts must be printed, on one side only and double-spaced, on A4 (210 x 297 mm) or equivalent paper and all pages should be membered. All margins must be at least 25 mm wide. Authors must submit **three paper copies** (print-out), including tables and figures, and are expected to retain another copy. **Original artwork** should only be submitted with the revised version of the accepted manuscript. The accepted final version of the manuscript must be submitted on a CD as a single file in Microsoft Word (.doc) or Rich Text Format (.rtf).

The text should be in roman (standard) type face throughout, except for genus and species names which must be formatted in *italics* (**bold italics** in taxa headings) and author's names in the list of references (not in other parts of the text!), which should be formatted in SMALL CAPITALS, LARGE CAPITALS may be used for main chapter-headings and SMALL CAPITALS, for subordinate headings. Footnotes and cross-references to specific pages should be avoided. Papers should conform to the following general layout.

Title page. A concise but informative full title plus a running title of not more than 40 letters and spaces, full name(s) and surname(s) of author(s), and full address(es) including e-mail address(es) if possible.

Abstract. The abstract is in English, composed of the title and a short text of up to 200 words. It should summarise the contents and conclusions of the paper and name all newly described taxa. The abstract is followed by up to 10 keywords, separated by hyphens, which are suitable for indexing. Some of the terms used in the title may be omitted from the list of keywords in favour of significant terms not mentioned in the title.

Introduction. A short introduction to the background and the reasons for the work.

Material and methods. Sufficient experimental details must be given to enable other workers to repeat the work. The full binominal name should be given for all organisms. The International Code of Zoological Nomenclature must be strictly followed. Cite the authors of species on their first mention.

Results. These should be concise and should not include methods or discussion. Text and tables should not duplicate the same information. The abbreviations gen. n., sp. n., syn. n. and comb. n. must be used to distinguish all new taxa, synonyms or combinations. Primary types must be deposited in a museums or similar institution. In taxonomic papers the species heading should be followed by synonyms, material examined, description, distribution, and comments. All material examined should be listed in similar, compact and easily intelligible format; the information should be in the same language in the text. Sex symbols should be used rather than "male" and "female" (text file: \$ = ♂. £ = ♀).

Discussion. The should not be excessive and should not repeat results nor contain new information, but should emphasize the significance and relevance of the results reported.

References. The autor-date system (name-year system) must be used for the citation of references in the text, e.g. White & Green (1995) or (White & Green, 1995). For references with three and more authors the form Brown *et al.* (1995) or (Brown *et al.*, 1995; White *et al.*, 1996) should be used. In the text authors' names have to be written in standard type face. However, in the list of references they should be formatted in SMALL CAPITALS (see below). The list of references must include all publications cited in the text and only these. References must be listed in alphabetical order of authors, in the case of several papers by the same author, the name has to be repeated for each reference. The title of the paper and the name of the journal must be given in full in the following style:

PENARD, E. 1888. Recherches sur le *Ceratium macroceros*. Thèse, Genève, 43 pp.

PENARD, E. 1889. Etudes sur quelques Héliozoaires d'eau douce. *Archives de Biologie* 9: 1-61.

MERTENS, R. & WERMUTH, H. 1960. Die Amphibien und Reptilien Europas. *Kramer, Frankfurt am Main*, XI + 264 pp.

HANDLEY, C. O. Jr 1996. Checklist of the mammals of Panama (pp. 753-795). In: WENZEL, R. L. & TIPTON, V. J. (eds). Ectoparasites of Panama. *Field Museum of Natural History, Chicago*, XII + 861 pp.

Tables. These should be self-explanatory, with the title at the top, organised to fit 122 x 180 mm.

Figures. These may be line drawings or half tones, not integrated in the text-file, and all should be numbered consecutively. Drawings and lettering should be prepared to withstand reduction to fit the page size of 122 x 170 mm. Magnification should be indicated with scale lines. Refrain from mixing drawings and half tones. Originals of figures (ink drawings, photographs, slides) should be submitted together with the revised version of the accepted manuscript. Original drawings will not be returned automatically. The *Revue suisse de Zoologie* declines responsibility for lost or damaged slides or other documents. If files of scanned figures are submitted, this should be clearly indicated on the print-out. Scanned line drawings must be saved as TIF files in bitmap mode with a resolution of at least 600 dpi. Half tone illustrations and photos must have at least 300 dpi resolution.

Legends to figures. These should be typed in numerical order on a separate sheet.

Proofs. Only page proofs are supplied, and authors may be charged for alterations (other than printer's errors) if they are numerous.

Offprints. All authors will receive a PDF file of their article, but no free offprints. Offprints may be ordered at current prices when the proofs are returned.

Correspondence. All correspondence should be addressed to:

Revue suisse de Zoologie, Muséum d'histoire naturelle, CP 6434, CH-1211 Genève 6, Switzerland.

Phone: +41 22 418 63 33 - Fax: +41 22 418 63 01. E-mail: rsz.mhn@ville-ge.ch

Home page RSZ: <http://www.ville-ge.ch/mhng/publication03.php>



SMALES, L. R. <i>Acanthocephala</i> including the descriptions of new species of <i>Centrorhynchus</i> (Centrorhynchidae) and the redescription of <i>Lueheia inscripta</i> (Westrumb, 1821) (Plagiorhynchidae) from birds from Paraguay South America	175-202
HOLLIER, J. An annotated list of the Orthoptera (Insecta) species described by Henri de Saussure, with an account of the primary type material housed in the Muséum d'histoire naturelle de Genève, Part 4: The Acridomorpha excluding the superfamily Acridoidea	203-219
HOLLIER, J. The Embioptera (Insecta) described by Henri de Saussure . . .	221-227
HERTACH, T. & NAGEL, P. Cicadas in Switzerland: a scientific overview of the historic and current knowledge of a popular taxon (Hemiptera: Cicadidae)	229-269
BESUCHET, C., CUCCODORO, G. & SABELLA, G. On the genera <i>Acanthobythus</i> Normand, 1930 and <i>Ceratobythus</i> Normand 1932 (Coleoptera: Staphylinidae: Pselaphinae)	271-280
MONOD, L., HARVEY, M. S. & PRENDINI, L. Stenotopic <i>Hormurus</i> Thorell, 1876 scorpions from the monsoon ecosystems of northern Australia, with a discussion on the evolution of burrowing behaviour in Hormuridae Laurie, 1896	281-346

Indexed in CURRENT CONTENTS, SCIENCE CITATION INDEX